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# HABITAT SELECTION AND BEHAVIOURAL PATTERNS OF SUMMERING CARIBOU IN THE MACKENZIE MOUNTAINS, N.W.T.

by

James Quayle

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE.

Department of Geography

Edmonton, Alberta
Fall 1994

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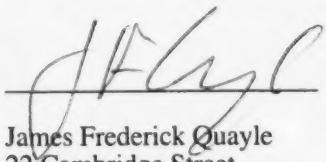

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis titled HABITAT SELECTION AND BEHAVIOURAL PATTERNS OF SUMMERING CARIBOU IN THE MACKENZIE MOUNTAINS, N.W.T. submitted by JAMES F. QUAYLE in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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DEDICATED TO:
My wife, Hilary,
and my parents,
Molly and Don

**Abstract**

Summer habitat selection of mountain caribou has received little attention in the past. This study was an investigation of the use and selection of summer habitat and the behavioural patterns of caribou near the Macmillan Pass, N.W.T. This study is unique in that it places habitat selection in a diurnal context.

Selection of habitat by summering mountain caribou involves partitioning between those resources that provide security and relief, and those that provide forage. This partitioning was investigated by counting pellet-groups, sampling phytomass, and evaluating topography in nine habitat-types on an unnamed mountain. Caribou use was greatest in high elevation habitat-types, which apparently offered advantages in terms of relief from insects and safety from predators. Caribou avoided areas with tall, dense shrubs, possibly as a strategy against stalking and ambushing by predators. There were no apparent relationships between caribou use, and phytomass of mosses, lichens, or graminoids; however, forbs appeared to have some influence on the selection of habitat-types.

Despite the seasonal abundance of forage in the spring and summer, the ability of caribou to feed is apparently constrained by the presence of blood-sucking and biting insects. The relationships between insects, temperature, and activity were investigated through collection of focal observations of caribou. Caribou followed a diurnal activity pattern in which they fed and travelled during the early morning and late evening, and rested and stood during the afternoon. Caribou minimized their distance to late-lying snowpatches in the afternoon, apparently to escape insects when temperatures were warmest, and harassment was most severe. Insect avoidance behaviour became more prevalent over the summer, indicated by an increase in the size of aggregations, and the amount of time spent standing.

Diurnal habitat patterns have been described in the literature, but seldom are they investigated in any depth. In an attempt to examine such patterns, focal observations of caribou habitat use were collected. Caribou displayed a distinct circadian rhythm of habitat use in which high elevation, steeply-sloped, northeasterly aspects were utilized in the afternoon while lower elevations, flatter slopes, and varied aspects were used in the morning and evening. This pattern was apparently driven by temperature and insect activity. Snowpatch habitat was selected almost exclusively at midday while evening and morning were characterized by a more varied assortment of habitats, and particularly forb meadows. Male caribou may have been venturing into subalpine habitats to feed during twilight, but females appeared to be restricted to alpine areas, presumably due to the vulnerability of calves to predation.

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# Introduction

## Rationale

Caribou (*Rangifer tarandus*) are unique among Cervids in North America in that both males and females produce and shed antlers annually. Although there has been some debate as to taxonomy, there are three sub-species of caribou found in Canada, each occupying a distinct latitudinal zone. Peary caribou (*R. t. pearyi)* inhabit the high Arctic islands, barren-ground caribou (*R. t. granti/groenlandicus*) inhabit the northern extremes of the continent, and woodland caribou (*R. t. caribou*), the subject of this thesis, currently occupy the most southerly distribution, inhabiting the boreal forest-tundra ecotone.

The range of *R. t. caribou* has diminished in the recent past. Caribou have been extirpated from nearly all of their former range in the lower forty-eight American states (Servheen & Lyon 1989), while in southern Canada, local survival is apparently threatened by resource exploitation and habitat destruction (Edmonds 1991, Racey *et al.* 1991). Because wintering caribou utilize stands of merchantable timber, their local persistence has come into conflict with logging interests (Darby & Duquette 1986, Stevenson 1991). This has created an obvious need for study of winter range; however, it may also have resulted in a consequent de-emphasis of the need for summer-based research. Although study of winter range has become predominant in the literature for many North American ungulates, the caribou is perhaps better adapted to life in the snow and cold than any other terrestrial mammal in the world (Kelsall & Telfer 1971). Furthermore, the woodland subspecies of caribou lives at the southern limit of the species distribution, where winter range would logically exert minimal influence as a limiting factor. From this perspective, caribou summer range is a topic worthy of greater attention than it has received.

Study of alpine summer habitat used by caribou is by no means easy. Cryptic pelage and sporadic distribution reduce the efficiency of aerial survey work. Aerial surveys of animals on mountain snowpatches in the afternoon have been attempted, but researchers admit such techniques have limited utility and reliability (Heard 1991). As an alternative, ground study is logistically challenging and physically demanding in mountainous areas. Hiking on steep slopes is strenuous, alpine weather can be fickle and unpredictable, and a researcher could conceivably work all day for very little return in terms of data. Furthermore, one might question the urgency of studying such inaccessible, inhospitable habitat, as it would seem unattractive to potentially disruptive human activities.

However, in light of the controversies and problems surrounding caribou summer habitat research, or perhaps in spite of them, a study of the alpine and subalpine habitat near the Macmillan Pass, Northwest Territories was undertaken in the summer of 1993 (Figure 1.1). Research took place on and around an unnamed mountain located south of the abandoned CANOL road and approximately 15 km east of Macmillan Pass (Fig. 1.2). This area was believed to lie within the summer range of the Redstone Herd, perhaps the largest herd of the mountain ecotype of woodland caribou in North America, numbering some 3000 - 4000 animals (R. Farnell, pers. comm.). Redstone caribou winter to the east, in the forested valleys and depressional areas along the Redstone River, and then disperse in spring, into the alpine tundra areas around Macmillan Pass to graze green shoots, forbs, and sedges (Farnell & Nette, 1981). It is not clear whether the study animals belong to the Redstone aggregation or whether they act as a small, independent metapopulation.

The term 'mountain caribou' will be used within the text of this paper in an attempt to differentiate the study animals from the more sedentary ecotype which occupies the boreal forest year-round.

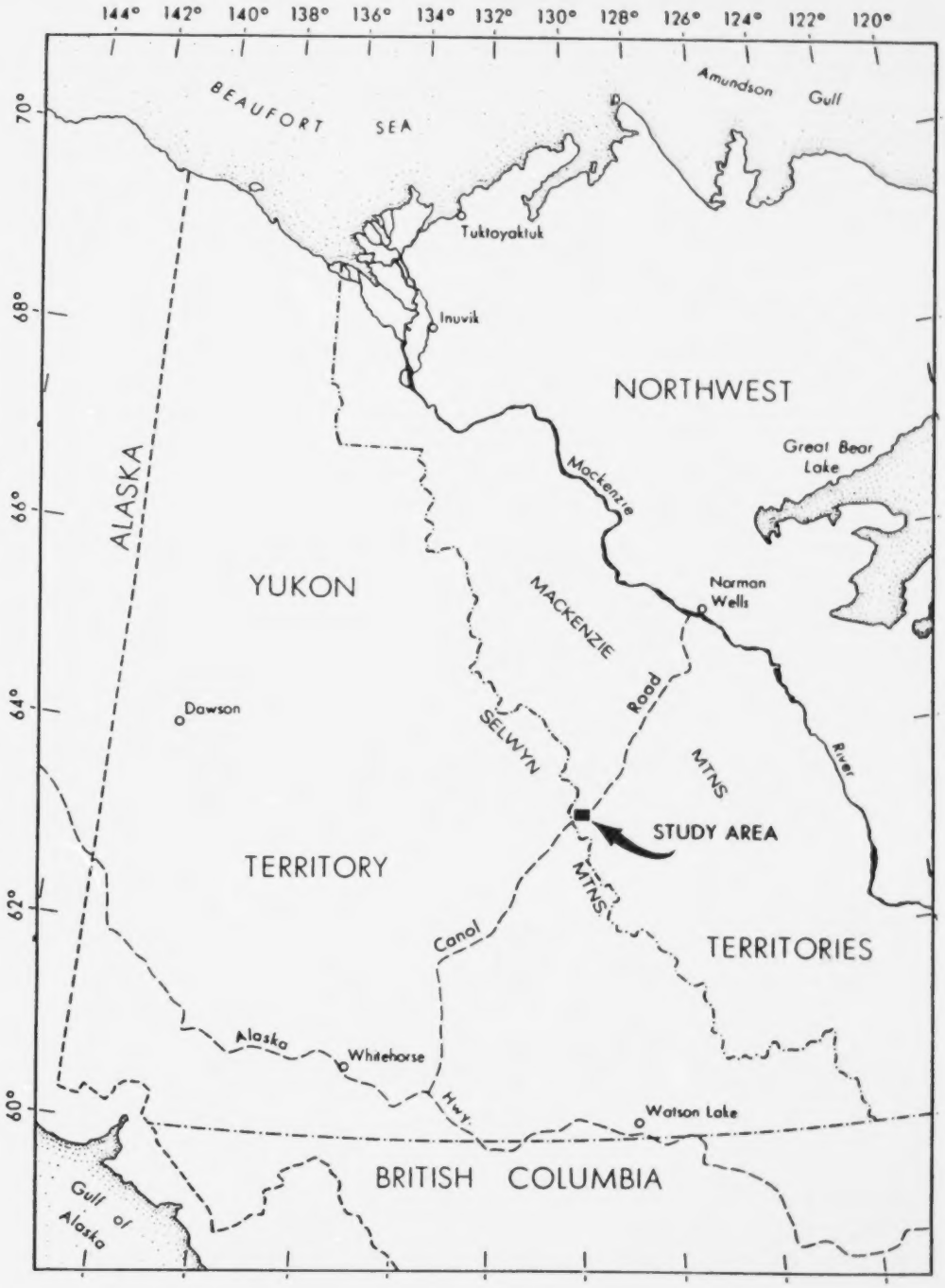


Figure 1.1. Location of study area.

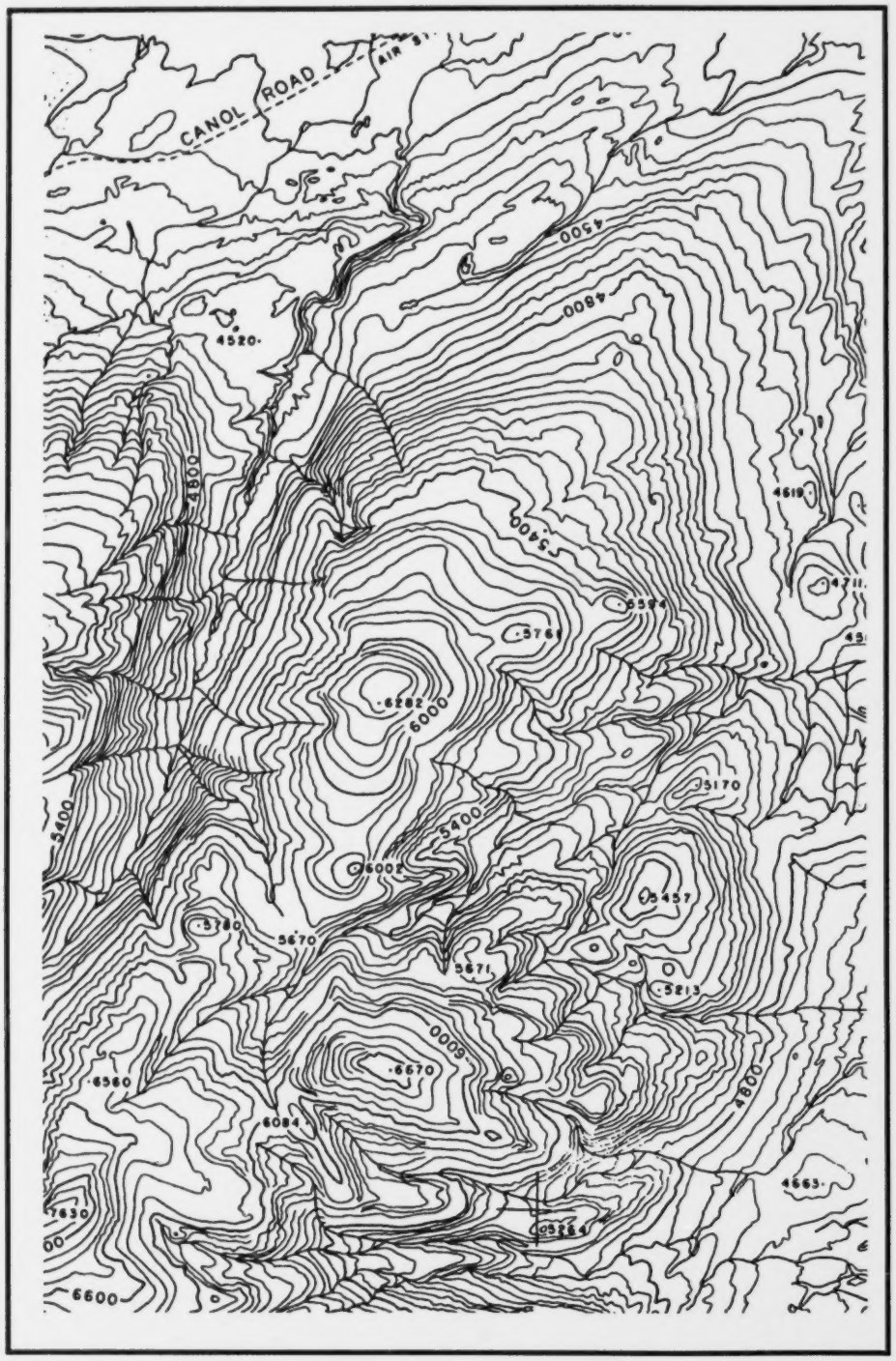


Figure 1.2. Topography of study area located on and around the central mountain (summit 6282 ASL). Scale is 1 to 50,000. Contours are in feet.

## Objectives and organization

The objective of the present study was to understand the process of summer habitat selection by mountain caribou. This was to be accomplished by investigating both the environmental factors that apparently influence habitat preference - temperature, insect abundance, forage availability, and threat of predation - and the behavioural and habitat selection responses of the caribou. For the most part, the investigation took place within a diurnal context to facilitate the sampling of repetitive daily environmental influence/response patterns.

The body of this thesis is broken into three papers, each dealing with a distinct aspect of caribou habitat selection. The first of these papers ("Selection of habitat-types by mountain caribou") is a study of habitat selection over the duration of the 1993 fly-season. This study attempts to relate habitat use, as determined through pellet-group counts to forage abundance and topographic features. The second paper ("Circadian activity budgeting and insect-harassment responses of mountain caribou") is an examination of the diurnal activity budgeting and insect avoidance behaviour as determined from direct observations of wild caribou. Investigation is also undertaken of gender-specific differences in activity budgets, and how these may change over the summer. The final paper ("Circadian patterns in summer microhabitat selection by mountain caribou"), follows a similar format, however, rather that comparing activities, it focuses on selection of specific habitat associations, and use of elevations, slopes, and aspects by caribou. Unlike the first paper which is based primarily on proxy information, this paper is based on observational data.

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# Selection of summer habitat-types by mountain caribou

## Introduction

Food preference and availability are important in the selection of habitat exercised by caribou (Kelsall 1968, Skoog 1968, White *et al.* 1975, Skogland 1980, Servheen & Lyon 1989). Summering caribou are known to favour areas characterized forbs, sedges, and willows, often in succession of the first availability of vegetation (Stelfox *et al.* 1978, Bloomfield 1979, Oosenbrug & Theberge 1980, Skogland 1980, Brown *et al.* 1986).

On warm, calm summer days, the caribou's apparent preference for green, succulent plants must be compromised when insect activity in moist meadows, wetlands, and riparian areas reaches unbearable levels (Skogland 1980, Roby 1986). At these times, mountain caribou are known to retreat to sparsely vegetated areas such as windy ridge tops and snowpatches for relief (Downes *et al.* 1986, Ion & Kershaw 1989). The threat of predator ambush, particularly to cows with calves in shrubby, riparian communities, provides further incentive to avoid these areas of abundant forage and to disperse into secure, high altitude habitats with superior vantages (Bergerud *et al.* 1984a, Jakimchuk *et al.* 1987, Seip 1992). It seems probable that selection of summer habitat by mountain caribou involves partitioning between those habitats that provide security and relief, and those that provide forage (Bergerud 1974, Bergerud *et al.* 1984b ).

It was the primary purpose of this study to investigate the selection of summer habitat by mountain caribou (*Rangifer tarandus caribou*) in an alpine area on the border of the Selwyn and Mackenzie Mountains, Northwest Territories using pellet-group transects. By comparing vegetation and physical characteristics with use of different habitat-types, it was possible to assess a caribou's prioritization of habitat needs in terms of forage requirements, relief from insects, and safety from predators.

## Study area

Research took place on an unnamed mountain 15 km east of the Continental Divide in Macmillan Pass. The Pass is an east-west running corridor which traverses the Mackenzie/Selwyn Mountains above timber-line. Concentrations of mountain caribou, belonging to the Redstone herd, occupy the vicinity of Macmillan Pass between June and September, but are rarely seen at other times of the year (Miller 1976, Farnell & Nette 1981).

The Macmillan Pass area experiences a continental climatic regime modified by an alpine environment. Mean annual precipitation is 490 mm, and snow may fall during any month of the year. July, with a mean monthly temperature of 10°C, is the warmest month of the year.

With regard to vegetation, Erect Deciduous Shrub Tundra dominates at low elevation. Plant communities are characterized by birch (*Betula glandulosa*) in association with lichens and mosses on drier sites, and several species of willow (*Salix* spp.) in association with mosses, sedges, and forbs on wetter sites.

Moderate to high elevation sites are frequently occupied by low-growing heath (*Cassiope tetragona*) interspersed within mats of lichens, particularly on rolling, moderately-sloped terrain. High elevation plateau areas appear as a rich, green mosaic of alpine and forb meadows, enriched by meltwater from late-lying snowpatches. On the windswept dome of the study mountain, cobble-dominated sorted circles lie adjacent to a sparsely vegetated lichen-grass community.

## Methods

*Habitat-type designation*

Transect blocks, each made up of six 100-m-long transects, were subjectively located in nine habitat-types on the shoulder of an unnamed mountain. Sites were selected on the north face as caribou tend to favor cool, north-facing slopes in summer (Oosenbrug 1976, Bloomfield 1979, Skogland 1980). An attempt was made to include all prominent plant communities mapped by Kershaw and Kershaw (1982) while maintaining an approximately evenly-spaced elevational gradient between the base and the summit of the mountain. Within each habitat type, transects were oriented parallel to one another in order to maximize vegetation homogeneity. Descriptions of each habitat-type included aspect, slope, elevation, topography, and proximity of ecotones.

*Phytomass collection*

Above-ground phytomass samples were collected in early August using nine quadrats which were randomly placed in each habitat-type. To speed sorting, a 10x10 cm quadrat was used for non-vascular plants while a larger 25x25 cm quadrat was used for all other live plants. All six transects within a habitat-type were sampled once, after which three transects were sampled a second time based on the roll of a die. Samples were sorted into mosses, lichens, graminoids, forbs and shrubs. All samples were dried in a 60°C oven before being weighed.

*Pellet-group counts*

All transects were surveyed for pellet-groups twice, once in early July and again in early August. During the first survey, all fecal matter was removed from the 4 m-wide belt transects. Pellet-groups were categorized on the basis of morphology as either: 1. a single, coalesced mass, 2. a discrete, scattering of pellets, or 3. a transitional or intermediate character.

*Data analysis*

All phytomass values were converted to $g \cdot m^{-2}$ and the time between clearing and resurveying of transects was standardized to 38 days in order to equalize the opportunity for caribou to use each habitat type. All pellet-group counts were converted from a value based on the area of the transect (400 $m^2$) to pellet-groups per hectare.

Analysis of variance (ANOVA) based on habitat-type was performed on pellet-group data sets for both July and August. Similar ANOVA's were performed on the phytomass data for shrubs, forbs, graminoids, lichens, mosses, and total phytomass.

## Results

*Physical characteristics*

Habitat-types selected for transect blocks occupied a range of plant communities and elevations from 1218 m to 1970 m (Table 2.1). The steepest study slope was on a late-lying snowpatch just below the summit dome; several other sites had slopes <1°. All habitat-types had northern aspects.

Table 2.1. Descriptions of nine habitat-types surveyed for pellet-groups in July and August.

| Plant Community | Terrain | Elev.(m) | Slope(°) | Aspect |
|---|---|---|---|---|
| Riparian willow | Riverbank | 1218 | <1 | - |
| Birch-moss | Hillside | 1316 | 5 | N |
| Birch-lichen | Plain | 1318 | <1 | - |
| Willow-forb | Lakeside | 1328 | <1 | - |
| Lichen-heath | Rolling hills | 1480 | 8 | NE |
| Lichen-heath | Alpine slope | 1650 | 5 | NW |
| Forb meadow | Alpine plateau | 1725 | 8 | N |
| Snowpatch | Alpine slope | 1880 | 22 | NE |
| Lichen-grass | Summit plateau | 1970 | <1 | - |

*Vegetation characteristics*

Variability within plant groups in a habitat-type was high - many standard deviations exceeded 70% of their associated mean values (Fig. 2.1a, 2.1b). This was a consequence of using a small sample size when variability inherent within the system was high. In order to make use of the data, values were assumed to reflect the grosser differences in phytomass among habitat-types. The least variability in phytomass occurred in the Forb Meadow, where the standard deviation was notably low for forbs.

With regard to relative amounts of phytomass, the Lichen-Grass habitat type had the lowest total phytomass, composed mainly of mosses and lichens (Fig. 2.1a, 2.1b). Woody plants were nearly absent from all the alpine habitats. Shrubs and graminoids were most abundant in the Willow-Forb habitat-type, despite a relatively low overall phytomass. Graminoids were also abundant in the Forb Meadow which also had the greatest forb phytomass. In contrast, forbs were most rare in the Birch-Lichen habitat-type even though this community had the highest overall phytomass, due to an abundance of shrubs, mosses, and lichens. Similarly, lichens in combination with shrubs constituted a large portion of the phytomass of both Lichen-Heath habitat-types. Between-group variance significantly exceeded within-group variance for phytomass of shrubs, forbs, graminoids, mosses, lichens and all plants ($F=2.22$ @ $p=0.04$, $F=6.19$ @ $p=0.00$, $F=2.30$ @ $p=0.03$, $F=3.93$ @ $p=0.00$, $F=8.39$ @ $p=0.00$, and $F=4.83$ @ $p=0.00$ respectively).

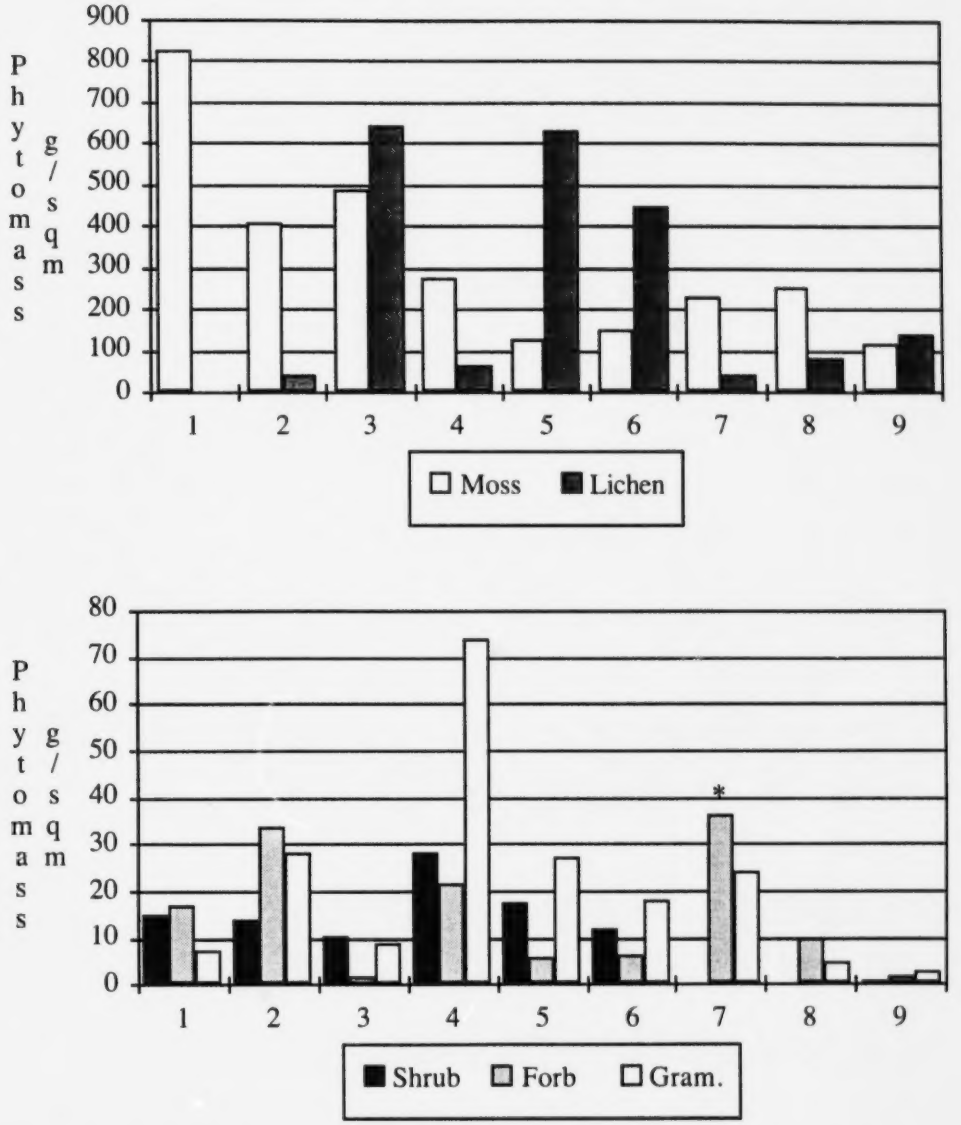


Figure 2.1a, 2.1b. Mean phytomass ($g \cdot m^{-2}$) (August 1993) of mosses, lichens, shrubs, forbs, graminoids in nine habitat-types, numbered from lowest to highest elevation. 1=Riparian Willow, 2=Birch Moss, 3=Birch-Lichen, 4=Willow-Forb, 5=Lichen-Heath, 6=Alpine Lichen-Heath, 7=Forb Meadow, 8=Snowpatch, 9=Lichen-Grass. Gram.=Graminoids. Standard deviation exceeds 70% of the mean value in all cases, except where * is shown.

*Pellet-group counts*

Generally, there was a direct relationship between pellet-groups and elevation (Fig. 2.2). In both early July and early August, the largest mean number of pellet-groups were recorded on the summit of the mountain while there was an absence of pellets in some low elevation habitat-types, specifically the Riparian Willow and Birch-Lichen.

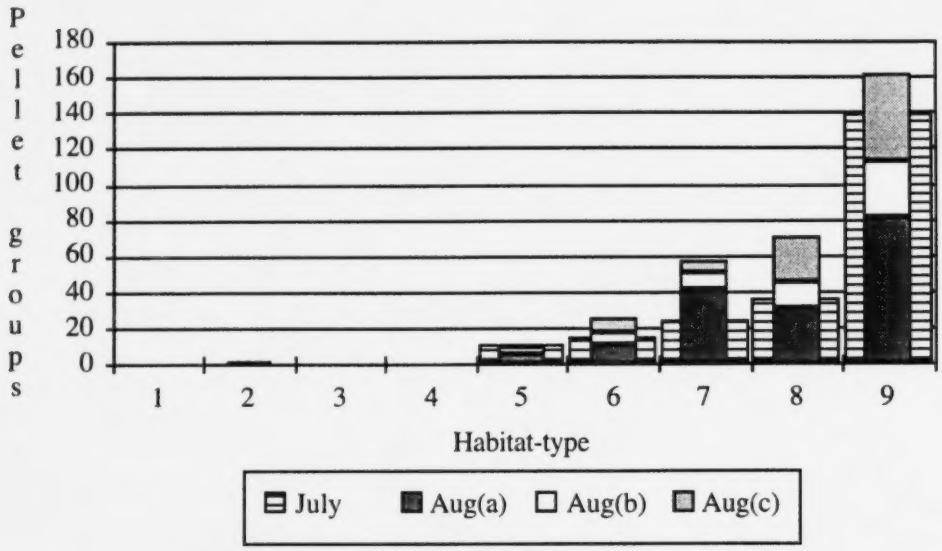


Figure 2.2. Mean caribou pellet-groups per hectare counted in nine habitat-types during early July and August 1993. 1=Riparian Willow, 2=Birch Moss, 3=Birch-Lichen, 4=Willow-Forb, 5=Lichen-Heath, 6=Alpine Lichen-Heath, 7=Forb Meadow, 8=Snowpatch, 9=Lichen-Grass. August pellet-groups are subdivided based on morphology into coalesced pellet-groups (a), transitional pellet-groups (b), and scattered pellet-groups (c). Standard deviation is less than 50% of the mean value for habitat-types 5 - 9.

Coalesced, scattered, and transitional pellet-groups were found in both July and August surveys; however, as pellets in the August survey were known to be deposited during July 1993, only these are presented in categories (Fig. 2.2). Scattered and transitional pellet-groups were absent from low elevation habitat types while there appeared to be a disproportionately large number of coalesced pellets-groups in the Forb Meadow habitat-type, which contained the greatest mass of forbs. Generally, the lower phytomass for all plants, and specifically shrubs, graminoids, mosses, and lichens in alpine habitat-types was accompanied by a higher abundance of pellet-groups (Fig. 2.1a, 2.1b, 2.2). There was significant variability in the mean number of pellet-groups among habitat-types, with minimal variability within each habitat-type ($F=30.44$ @ $p=0.00$, $F=45.94$ @ $p=0.00$ for July and August respectively).

**Discussion**

Unlike track counts, pellet-group counts are not dependent on the hardness of the ground surface, or on the difficulties of distinguishing between sign of separate animals (Fischer *et al.* 1977). In contrast to both ground and aerial surveys, pellet-group counts can be an inexpensive way to assess the relative habitat use of an animal virtually *in absentia*. However, after utilizing this technique on the Boothia peninsula, Fischer *et al.* (1977) point out that the interpretation of their results may be clouded by the high mobility of barren ground caribou, and the possibly-erroneous assumption that the number of pellet groups found within a habitat indicate the amount of time an animal spends there. Nonetheless, for over 50 years, ungulate pellet-group counts have successfully been employed by many researchers as an index of relative habitat use (e.g. Bennet *et al.* 1940, Rogers *et al.* 1950). In addition, although barren-ground caribou tend to be a highly

mobile animal, mountain caribou are essentially sedentary in the summer time (Brown *et al.* 1986).

Because the study area is believed to be used exclusively as summer range by caribou, the early July pellet-group survey is essentially based on pellets dropped in previous summers, and the similarity between July and August pellet data implies a consistent trend in use of the nine habitat-types (Fig. 2.2). The only exception was in the alpine Lichen-Grass habitat-type in which there were more pellets counted in August than in July. Most likely, this disparity was due to the greater age and exposure of the pellet-groups counted in early July which frequently appeared scattered by snowmelt run-off and animals, particularly in heavily-used habitats. This made it difficult to correctly identify discrete pellet groups. Thus, it is possible that the July count was an overestimate of habitat use relative to the August count, even though the numbers may still be an accurate reflection of the relative use among habitat-types.

Alpine habitat-types were used more than low elevation ones (Fig. 2.2). Habitat use was greatest in habitat-types which had the highest elevations and the steepest slopes, with the exception of the Lichen-Grass habitat-type. The Lichen-Grass habitat-type was on the flattened summit of the mountain. It had the heaviest use, the highest elevation and a negligible slope (Table 2.1; Fig. 2.2). Caribou have been reported to seek ridge tops and snowpatches in the Mackenzie Mountains to apparently take advantage of wind conditions that are unfavorable to blood-sucking insects (Gill 1976, Ion & Kershaw 1990). This tendency was demonstrated by the high use of the Snowpatch habitat-type which likely provided a sanctuary from mosquitos and flies. An inverse relationship has been reported between elevation and insect activity, and thus summering caribou avoid insect pests by utilizing high elevation areas in west central Alberta, central British Columbia, and the eastern Yukon (Stelfox *et al.* 1978, Bloomfield 1980, Downes *et al.* 1976). Perhaps, the Lichen-Grass habitat-type provided exposure to wind due to its high elevation and exposure without making it necessary for animals to utilize a steep slope to find relief from insects. In light of this, the apparent selection of habitat-types with steep slopes may be nothing more than the result of the intuitively-obvious correlation between slope and elevation. This is supported by Oosenbrug (1976) who found caribou to have a preference for high elevations, but also for "flat-to rolling terrain" with slopes of <20°.

Antipredator advantages must also be considered in attempting to explain the heavy use of the Lichen-Grass habitat-type. The largest groups of caribou in the study area were post-calving aggregations of cows with calves. It has been suggested that the formation of these 'nursery bands' is an antipredator behaviour to protect vulnerable calves, and so it is likely that these bands would select secure habitats with good visibility and ready access to escape terrain (Bergerud 1974, Jakimchuk *et al.* 1987). Caribou space themselves out in summer and seek high elevation areas for security from predators (Bergerud *et al.* 1984a). They find safety in elevation when alternate prey for resident predators, specifically moose, occur in valley bottoms because caribou at high elevation will be less likely to encounter predators seeking moose (Seip 1992). Moose were sighted on several occasions in the low elevation, willow-dominated habitats around the study mountain. In contrast, the Lichen-Grass habitat-type occurs at the summit of the mountain, the highest location in the study area, providing space and superior visibility to avoid ambushing and stalking by predators.

Gill (1978) conducted counts of individual caribou pellets in the Macmillan Pass and found little connection between preferred communities and phytomass. This study achieved similar results concerning the lack of an obvious relationship between phytomass and habitat use. This may stem, in part, from the relatively small number of samples used. However, those communities with the least phytomass had the greatest evidence of use (Fig. 2.1a, 2.1b, 2.2). This is coincident with other studies which show that consumption of shrubs and lichens by caribou may reach its annual minimum in summer (Stelfox *et al.* 1978, Bloomfield 1979). In contrast, Skogland (1980) found a significant correlation between above-ground phytomass and time spent feeding in a vegetation type when animals are allowed to express selection uninterrupted by insect harassment. In the same

study, Skogland found that forbs were the most selected of any plant in alpine areas, a finding echoed by Stelfox *et al.* (1978) and Bloomfield (1979). This study is in agreement that the presence of forbs is a highly significant factor in summer habitat selection.

The Forb Meadow habitat-type had the greatest forb phytomass, occurring at 1725 m on a moist plateau beneath a steep snowy slope. Because caribou are opportunistic feeders, taking advantage of new growth as it appears, such areas become especially attractive to them (Gill 1978, Stelfox *et al.* 1978, Bloomfield 1979, Skogland 1980). August pellet data from the Forb Meadow supports this idea, with a large number of pellets of a coalesced morphology associated with lush, green forage (Fig. 2.2).

A large number of coalesced pellet-groups were also found in the Lichen Grass habitat-type, despite minimal forb phytomass (Fig. 2.1b, 2.2). Perhaps some of the appeal of this habitat-type, in addition to insect relief and security, is its proximity to the Forb Meadow. An animal could take advantage of the topographic and meteorological benefits of the Lichen-Grass during the heat of the day, and then make a visit to graze on the nearby Forb Meadow when conditions were favorable. The large number of coalesced pellets in the Lichen Grass habitat-type may be from resting animals, having returned from feeding visits to more lush communities. Such behavior patterns have previously been reported (Archibald 1973, Ion 1986).

Shrubs, particularly willow, have been suggested as preferred summer forage for caribou; however, the results of this study indicate shrub phytomass was low or absent where use was high. In fact, the only communities where both shrubs and caribou occurred in any abundance were the Lichen- and Alpine-Heath habitat-types in which the dominant shrubs (*Cassiope tetragona* and *Vaccinium uliginosum*) were low growing. Jakimchuk *et al.* (1987) demonstrated that cows with calves tended to avoid riparian areas with tall, concealing shrubs. Shrubs were absent at high elevations, resulting in higher visibility for cautious cows, as well as a lack of concealing cover for ambushing or stalking predators. It is likely that animals in post-calving aggregations, which contained the largest concentrations of caribou in the area, would select safe habitat, and this was reflected in the abundance of pellets found in open areas.

## Conclusions

1. In general, summering mountain caribou used habitat-types at higher elevations more heavily than those at lower elevations. This was likely due to the inverse relationship between elevation and insect activity.
2. In general, habitat-types with steeper slopes were used more frequently than those with lower slope angles; however, the most heavily used habitat-type had a slope of <1°. This implies that use of habitat-types with steep slopes may be no more than a product of the correlation between altitude and slope.
3. The most heavily used habitat-type, Lichen-Grass, offered advantages in terms of insect relief, high visibility of predators, and reasonable proximity to forage.
4. Summering caribou subject to insect harassment and potential predation, tend to occupy habitat-types where plant phytomass was lowest and concealing shrubs were absent.
5. Forb phytomass appeared to exert some influence over caribou distribution. Although summering caribou may avoid insects and predation as their first priority, the abundance of coalesced pellets found in the dry, barren Lichen-Grass habitat-type suggested that caribou made frequent feeding visits to more lush habitat-types.

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# Circadian activity budgeting and insect-harassment responses of mountain caribou.

## Introduction

Summer is a time of body replenishment from the previous winter and preparation for the winter to come. For caribou, the exposure of fresh, green vegetation in the spring is accompanied by an increase in nutritional requirements with critical implications for reproduction and recruitment - cows produce milk for new calves, juveniles resume body growth after the winter hiatus, and bulls begin developing the antlers and body size that will decide their mating status in the coming rut (Skoog 1968, Fisher *et al.* 1976). Despite an abundance of new forage to meet these physiologic demands, the opportunity for caribou to feed in summer is constrained by the presence of mosquitoes, tabanids ("bulldogs"), and oestrids (warble flies and nose bots) which force caribou to seek relief habitat when insects are active. It is to the possible detriment of caribou that relief areas, such as snowpatches, beaches, sandpits, gravel roads, windy ridge tops, and sections of ice, are generally characterized by an absence or paucity of vegetation, making feeding difficult, if not impossible (Kelsall 1968, Bergerud 1974, Roby 1978, Stelfox *et al.* 1978, Helle 1980, Downes *et al.* 1986, Ion & Kershaw 1989).

In addition to displacing caribou from desirable feeding areas, biting insects elicit behavioural responses from their prey. Individuals bothered by mosquitos and tabanids will engage in tail wagging, pawing, head-shaking, shivering, biting, bucking, and running (Roby 1978, Downes 1984, Ion 1986). When harassment reaches an extreme, a caribou may assume the so-called "insect stance", frozen with its limbs locked, head down, and snout protected against the ground (Banfield 1954, Kelsall 1968, Thomas & Kiliaan 1990). Perhaps the most violent insect avoidance behaviour is that associated with oestrids in which caribou may leap, buck, flatten themselves to the ground, and race wildly across the landscape (Banfield 1954, Kelsall 1968, Thomas & Kiliaan 1990). On a larger scale, caribou will form aggregations, when they are bothered by mosquitos and "bulldogs", in an apparent attempt to swamp the attackers with hosts thereby lessening the torment of each individual (Roby 1978, Helle & Tarvainen 1984); however, the presence of a single oestrid may cause an entire group of caribou to flee and disperse (Kelsall 1968, Downes *et al.* 1986). Such activities are not only energy intensive, but are also disruptive and diminish the time available for feeding.

Thus, for caribou, summer is a time of temporal partitioning between insect-avoidance and feeding activities (Bergerud 1974). In fact, Reimers (1980) suggests that the growth and fattening of caribou has less to do with summer range characteristics than it has to do with activity patterns. Similarly, Thomas & Kiliaan (1990) state that harassment by bot and warble flies is more important to the physical condition of an animal than any reactions caused by the parasitic larvae. This study examines activity budgeting and avoidance behaviour of mountain caribou near the Macmillan Pass, Northwest Territories.

## Study area

Research took place on an unnamed mountain approximately 15 km east of Macmillan Pass (Lat. 63° 18', Long. 130° 17'). The Pass is an east-west running corridor which crosses through the Mackenzie and Selwyn mountain ranges at the Yukon/N.W.T. border. At 1300 m, the Pass, and much of the surrounding area, is above timberline. The study mountain provides an elevational and vegetation gradient ranging from shrub birch and willow in surrounding valleys through heathlands, forb and alpine meadows at moderate elevations (1500 - 1750 m) up to epilithic lichen and terricolous lichen-grass communities at the summit (1970 m). Patches of bare rock and late-lying snow are also found at high elevation.

Mountain caribou, believed to be part of the Redstone herd, utilize areas of the Macmillan Pass for summer range, and are known to frequent high elevation areas, windy ridgetops, and late-lying snowpatches, apparently as part of their relief habitat, avoiding insects and high summer temperatures (Archibald 1975, Miller 1976, Urquhart & Urquhart 1977, Farnell & Nette 1981, Kershaw & Kershaw 1983, Ion & Kershaw 1989).

## Methods

*Survey technique*

After a brief reconnaissance flight in a small airplane, an unnamed study mountain was selected and searched on foot for caribou. Nearly all the animals seen occurred above 1600 m and so mountain camps were established to facilitate high elevation study. At the start of each day, binoculars were used to search large areas of the study mountain for caribou. The first animal encountered was used as a subject, and studied for as long as possible. Animals were observed through a spotting scope at a sufficient distance so as not to disturb them. The excellent visibility of the tundra landscape at high elevation facilitated observation of many animals simultaneously, particularly when they were sedentary and/or discretely grouped.

*Activity budgets*

The amount of time a focal animal spent standing, lying, feeding, and travelling was recorded to the nearest minute. Most groups were small enough, or similar enough in their activities that two observers could manage to collect data on all visible animals. On the few occasions when this was not possible and groups became too large, instantaneous scan samples were utilized (Altmann 1974). All observations were grouped into ten minute blocks.

Each ten minute observation block was assigned one activity, either lying, standing, travelling, or feeding, depending on which activity occupied the majority of the ten minutes. These modified blocks were then grouped according to time of day into four four-hour time categories beginning at 0700 and ending at 2300 h. Chi-squared tests (Sokal & Rohlf 1981) were then performed in an attempt to determine whether activity budgeting at different times of day was independent of sex. A larger data set, which included many unsexed animals was used for a similar test which evaluated the null hypothesis that there was no difference between activity budgeting during the first and second half of the field season.

*Harassment responses*

The number of caribou in each group and the estimated distance of each animal to the nearest snowpatch were also recorded at ten minute intervals. Observations were later grouped according to time of day into four subsets ranging from 0700 to 2300 h. Separate analyses of variance (ANOVA) were then performed on each data subset to investigate differences based on the sex of the animals, and whether observations were collected during the first or last half of the summer (Wilkinson 1988).

Data were also collected on individual harassment responses, including tail wagging, ear flicking, head tossing, shivering, stamping, biting, pawing, kicking, rearing, bucking, and running. Animals in a continual state of torment, and those displaying the "insect stance" were also noted. Using a simple scale of response severity, each observed insect-avoidance behaviour was assigned a numeric value (Table 3.1). These were then summed for each animal in each ten minute period and classified as mild (sum total of 1 - 3), moderate (sum total of 4 -7), or severe (sum total greater than 8) harassment. Harassment index values were then used as the basis for frequency histograms of diurnal harassment patterns.

Table 3.1. Index values of various behavioural responses of caribou to insect harassment.

| Index Value | Insect-harassment Response |
|---|---|
| 1 | Tail-wagging, Ear-flicking, Shivering |
| 2 | Stamping, Kicking, Head-tossing, Biting |
| 3 | Bucking, Running, "Insect stance" |
| 10 (maximum) | Continuous avoidance |

*Meteorological conditions*

Temperature and windspeed were recorded in association with each 10 minute behavioural observation using hand-held equipment, and cloud cover was noted. Two automated dataloggers were also established - one on a steep, sparsely vegetated slope at 1880 m, and the other in a rich alpine meadow at 1725 m. These continuously collected temperature and windspeed data were averaged over 2 hour intervals.

*Relationships*

Pearson's correlation coefficients were calculated to test the strength of the relationships among the following variables:

1. Air temperature (recorded with hand-held equipment)
2. Windspeed (recorded with hand-held equipment)
3. Cloud cover
4. Group size
5. Percent of time lying
6. Percent of time standing
7. Percent of time travelling
8. Percent of time feeding
9. Harassment index value
10. Estimated distance to nearest snowpatch
11. Time of day

## Results

*Activity budgets*

Female and male caribou varied significantly in activity budgeting between 0700 and 1500 h, and 1900 and 2300 h (Table 3.2). In contrast, during the period between 1500 and 1900 h, there was no significant difference between their activities. However, both sexes of caribou appeared to follow distinct circadian activity patterns, feeding and travelling in the early morning and evening, and spending the afternoon standing and lying (Fig. 3.1a, 3.1b). In general, females appeared to spend a greater amount of the day standing, while males spent a larger portion lying down. A large portion of females were seen feeding in the late evening, however it was not possible to compare this to male feeding patterns as few observations were collected of males in the early morning and late evening. Females travelled in the early morning whereas males travelled more throughout the day and into the evening.

Table 3.2. Summary of results of chi-squared test based on activity budgets of male and female caribou at different times of day. Observations were collected between 26 June and 1 August.

| Time Period | Chi-Squared | DF | Alpha | $H_0$ ? |
|---|---|---|---|---|
| 0700-1059 | 57.52 | 3 | <0.05 | Reject $H_0$ |
| 1100-1459 | 434.02 | 3 | <0.05 | Reject $H_0$ |
| 1500-1859 | 1.78 | 3 | >0.05 | Accept $H_0$ |
| 1900-2300 | 8.47 | 3 | <0.05 | Reject $H_0$ |

DF: degrees of freedom
$H_0$: there is no significant difference between the activity budgets of male and female caribou.

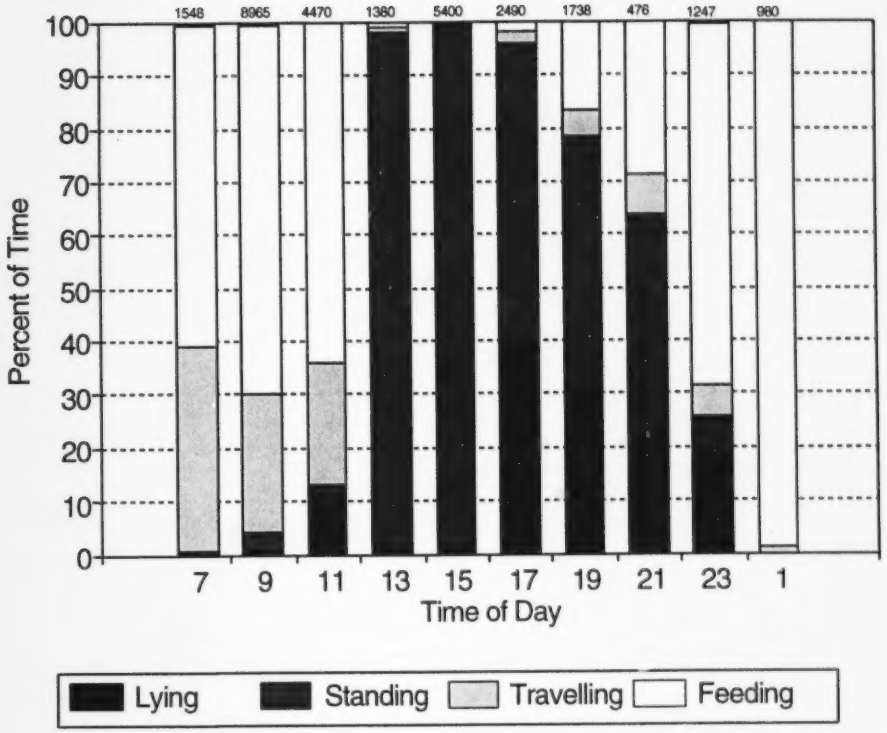


Figure 3.1a. Activity budget of female caribou, 26 June to 1 August 1993. Each numeral on the time of day scale represents observations for the two previous hours. Inset values are total number of animal observation minutes at each time.

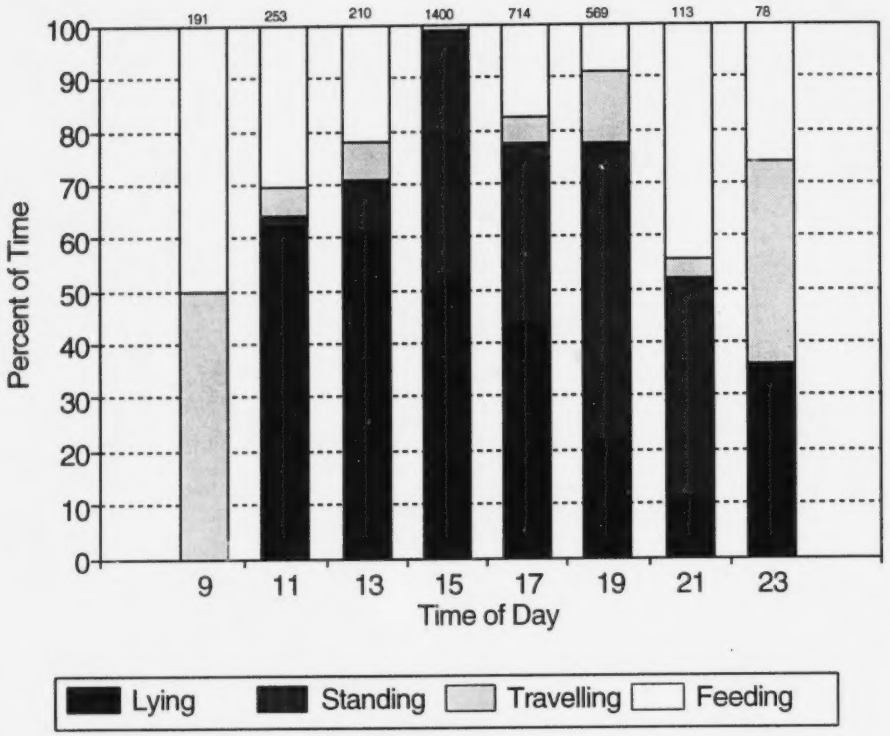


Figure 3.1b. Activity budget of male caribou, 26 June to 1 August 1993. Each numeral on the time of day scale represents observations for the two previous hours. Inset values are the total number of animal observation minutes at each time.

Activity budgets significantly changed between the first and second halves of the season at all times of day (Table 3.3). The circadian pattern of eating and travelling in the morning and evening was evident throughout the season, but a major shift occurred from lying down to standing up in the afternoon hours (Fig. 3.2a, 3.2b). Feeding and travel remained confined to the early morning and late evening, however, travel shifted from the morning to the evening in the second half of the summer.

Table 3.3. Summary of results of chi-squared test based on the activity budgets of caribou at different times of day throughout the season. Observations were collected between 26 June and 1 August 1993.

| Time Period | Chi-Squared | DF | Alpha | $H_0$ ? |
|---|---|---|---|---|
| 0700-1059 | 150.70 | 3 | <0.05 | Reject $H_0$ |
| 1100-1459 | 1918.55 | 3 | <0.05 | Reject $H_0$ |
| 1500-1859[1] | 48.07 | 1 | <0.05 | Reject $H_0$ |
| 1900-2300[2] | 42.56 | 1 | <0.05 | Reject $H_0$ |

[1]:excludes travelling and feeding which were absent.
[2]:excludes lying down and standing which were absent.
DF: degrees of freedom
$H_0$: there is no significant difference between the activity budgets of caribou observed in the first half of the summer and those observed in the last half.

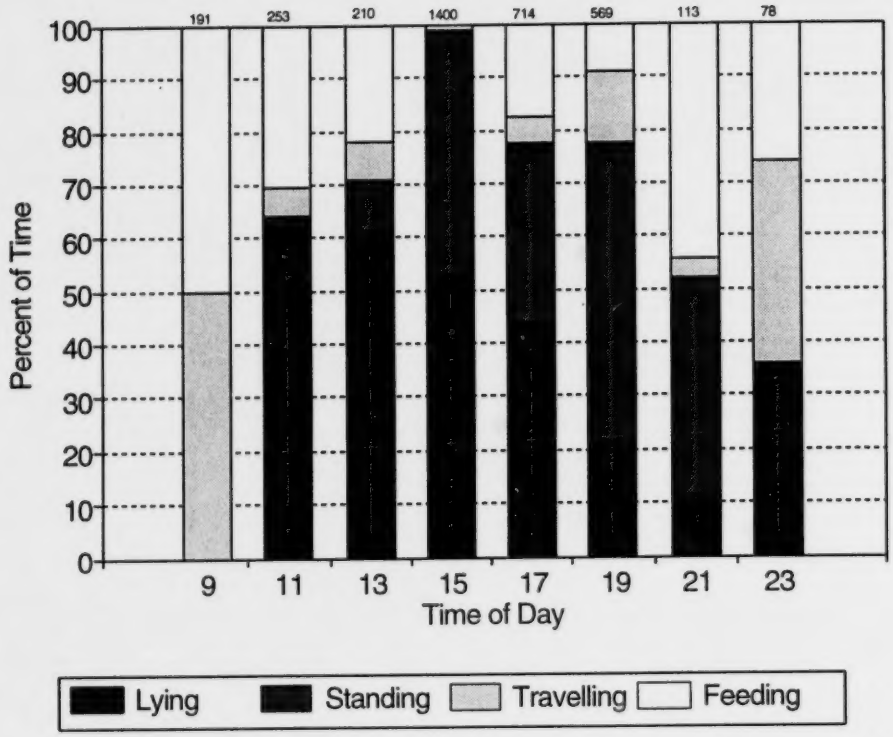


Figure 3.2a. Activity budget of caribou, 26 June to 15 July 1993. Each numeral on the time of day scale represents observations for the two previous hours. Inset values are the total number of animal observation minutes at each time.

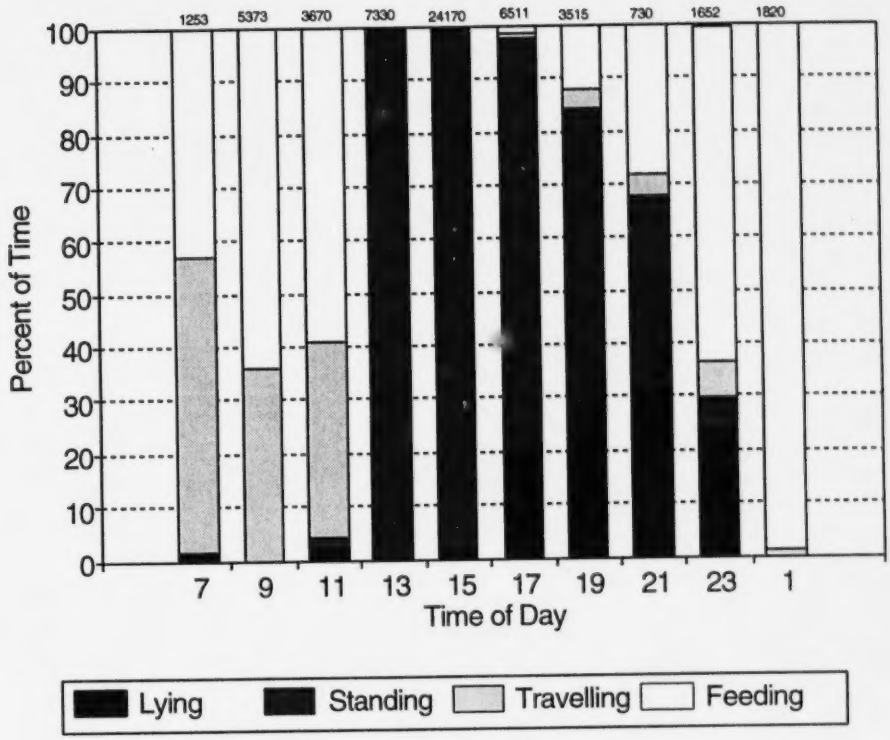


Figure 3.2b. Activity budget of caribou, 15 July to 1 August 1993. Each numeral on the time of day scale represents observations for the two previous hours. Inset values are the total number of animal observation minutes at each time.

*Harassment response*

Harassment index values revealed two peaks of harassment during the day (Fig. 3.3). Harassment of both males and females peaked between 0900 and 1100 h and again between 1700 and 1900 h. Both these times were also characterized by a higher frequency of severe harassment responses. A larger percentage of observations of harassed males were obtained relative to females, despite the substantially smaller sample size of males. Change in harassment response over the summer could not be reliably investigated due to small sample sizes at crucial times during the first half of the season.

Both sexes of caribou were furthest from snowpatches during the morning and evening, and were nearest during the late morning and afternoon (Fig. 3.4). For the majority of the day, their was no significant difference between the distance of males and females to snowpatches (Table 3.4); however, between the first and second half of the season, there was a significant decrease in the distance to snowpatches between the hours of 0700 and 1059, and 1500 and 1859 (Table 3.5).

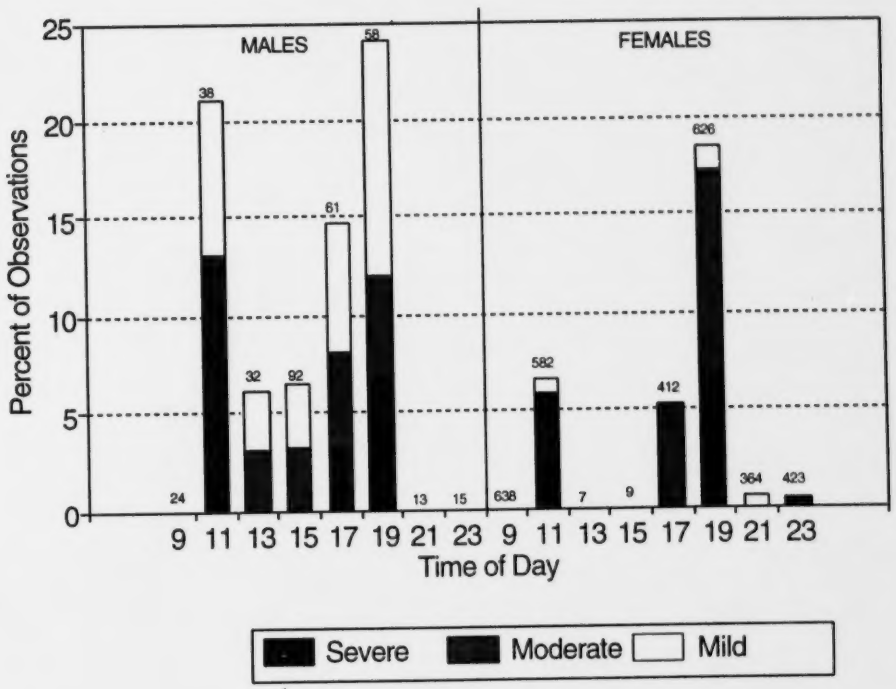


Figure 3.3. Hourly changes in harassment for male and female caribou, 26 June to 1 August 1993. Bars represent only that percentage of ten-minute observations where harassment values exceeded zero. Bars are subdivided based on whether harassment was classed as mild, moderate, or severe. Each numeral on the time of day scale represents observations for the two previous hours. Numerals at the top of each bar represent the number of observations.

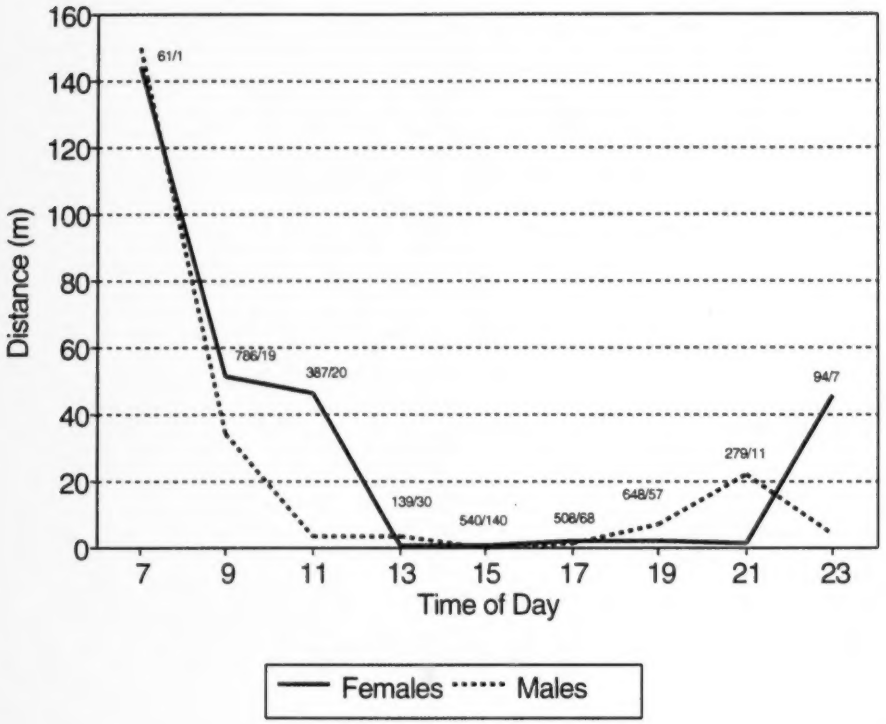


Figure 3.4. Hourly changes in mean distance of caribou to snowpatch (relief habitat) by sex, 26 June - 1 August 1993. Each numeral on the time of day scale represents observations for two previous hours. Annotated numerals represent the number of observations for females and males respectively.

Table 3.4. Summary of ANOVA based on the distance of male and female caribou to snowpatches (relief habitat) at different times of day. Observations were collected between 26 June and 1 August 1993.

| Time Period | Sex | Mean Distance | SD | n | F-ratio | p | $H_0$ ? |
|---|---|---|---|---|---|---|---|
| 0700-1059 | F | 48.91 | 50.45 | 1173 | | | |
| | M | 17.69 | 26.87 | 39 | 14.78 | 0.000 | Reject $H_0$ |
| 1100-1459 | F | 0.22 | 4.28 | 679 | | | |
| | M | 0.50 | 2.84 | 170 | 0.65 | 0.421 | Accept $H_0$ |
| 1500-1859 | F | 1.73 | 12.22 | 1156 | | | |
| | M | 3.66 | 19.85 | 125 | 2.44 | 0.119 | Accept $H_0$ |
| 1900-2300 | F | 11.94 | 24.37 | 373 | | | |
| | M | 14.78 | 33.39 | 18 | 0.22 | 0.637 | Accept $H_0$ |

SD: standard deviation.
n: number of observations.
p: probability that $H_0$ is true.
$H_0$: there is no significant difference between the distance to the nearest snowpatches of male and female caribou.

Table 3.5. Summary of ANOVA based on the distance of individual caribou to snowpatches (relief habitat) at different times of day throughout the season. Observations were collected between 26 June and 1 August 1993.

| Time Period | Half | Mean Distance | SD | n | F-ratio | p | $H_0$ ? |
|---|---|---|---|---|---|---|---|
| 0700-1059 | 1 | 54.13 | 55.08 | 1693 | | | |
| | 2 | 56.55 | 42.24 | 597 | 0.95 | 0.329 | Accept $H_0$ |
| 1100-1459 | 1 | 2.26 | 12.5 | 149 | | | |
| | 2 | 0.00 | 0.00 | 3555 | 116.98 | 0.000 | Reject $H_0$ |
| 1500-1859 | 1 | 2.79 | 9.83 | 53 | | | |
| | 2 | 1.48 | 11.03 | 2057 | 0.737 | 0.391 | Accept $H_0$ |
| 1900-2300 | 1 | 30.50 | 30.50 | 10 | | | |
| | 2 | 10.65 | 10.65 | 515 | 7.09 | 0.008 | Reject $H_0$ |

Half 1: 26 June - 15 July 1993
Half 2: 16 July - 1 August 1993
SD: standard deviation.
n: number of observations.
p: probability that $H_0$ is true.
$H_0$: there is no significant difference between the distance of caribou to the nearest snowpatches during the first half and the last half of the season.

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Group size at the beginning of the fly season was largest and most variable in the morning, and smallest and least variable in the afternoon and evening (Fig. 3.5). In contrast, after 15 July, group size was largest and most variable in the afternoon, and smallest in the morning and evening. Group size increased significantly over the summer during all time periods between 1100 and 2300 h (Table 3.6).

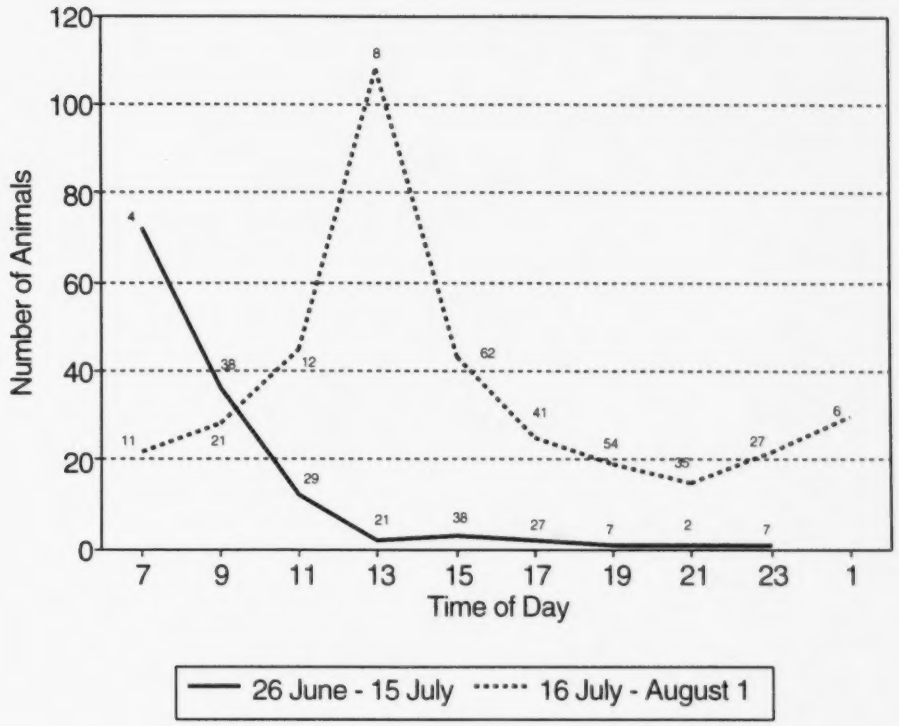


Figure 3.5. Daily changes in mean group size, 26 June to 15 July and 16 July to August 1 1993. Each numeral on the time of day scale represents observations for two previous hours. Annotated numerals represent the number of observations.

Table 3.6. Summary of ANOVA based on caribou group size at different times of day throughout the season. Observations were collected between 26 June and 1 August 1993.

| Time Period | Half | Mean Size | SD | n | F-ratio | p | $H_0$ ? |
|---|---|---|---|---|---|---|---|
| 0700-1059 | 1 | 25 | 36 | 67 | | | |
| | 2 | 34 | 22 | 33 | 1.63 | 0.205 | Accept $H_0$ |
| 1100-1459 | 1 | 3 | 1 | 59 | | | |
| | 2 | 51 | 56 | 70 | 42.56 | 0.000 | Reject $H_0$ |
| 1500-1859 | 1 | 2 | 0 | 34 | | | |
| | 2 | 22 | 21 | 95 | 37.93 | 0.000 | Reject $H_0$ |
| 1900-2300 | 1 | 1 | 0 | 9 | | | |
| | 2 | 18 | 24 | 62 | 4.26 | 0.043 | Reject $H_0$ |

Half 1: 26 June - 15 July 1993
Half 2: 16 July - 1 August 1993
SD: standard deviation.
n: number of observations.
p: probability that $H_0$ is true.
$H_0$: there is no significant difference between the size of caribou groups during the first half and the last half of the season.

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*Meteorological conditions*

At 1880 m, the daily temperature pattern was characterized by an increase in air temperature from 0800 until approximately 1600 h when it stabilized, and began to drop by 2000 h (Fig. 3.6). Windspeed followed a similar but steeper pattern, likely due to a lag in response to temperature.

For the duration of the study, temperature minima and maxima from dataloggers at both 1725 and 1880 m varied little, occupying a range of approximately 20 °C (Fig. 3.7). Throughout the study, the minimum temperatures obtained at 1725 m, a rich alpine meadow, appeared to be gradually warming.

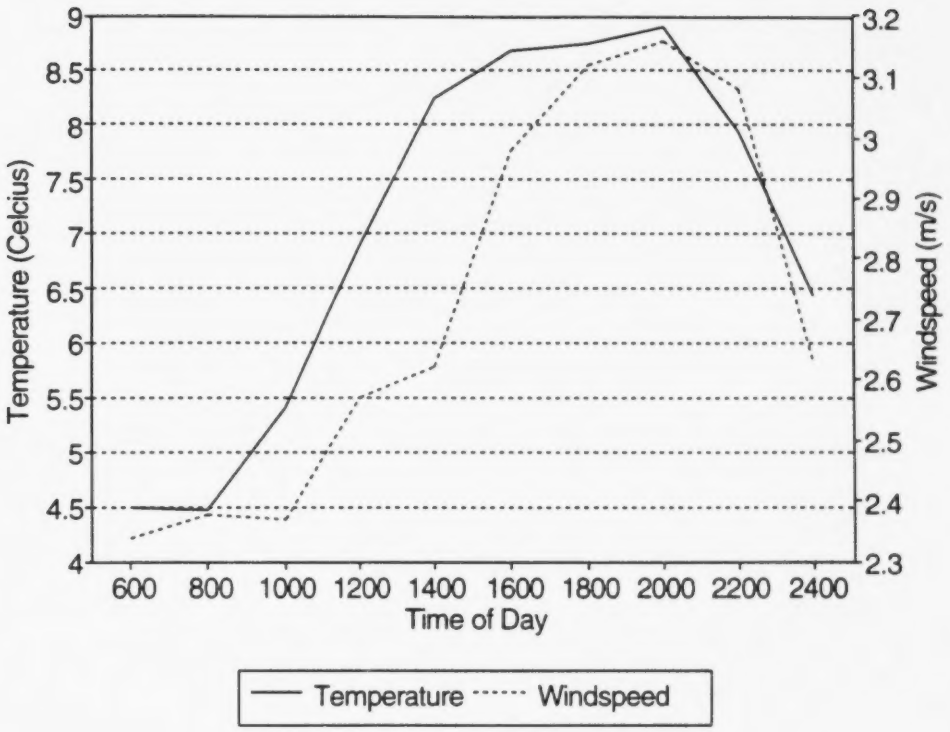


Figure 3.6. Hourly changes in mean temperature and windspeed at two hour intervals. Data were recorded by datalogger on slope at 1880 m between 26 June and 1 August 1993.

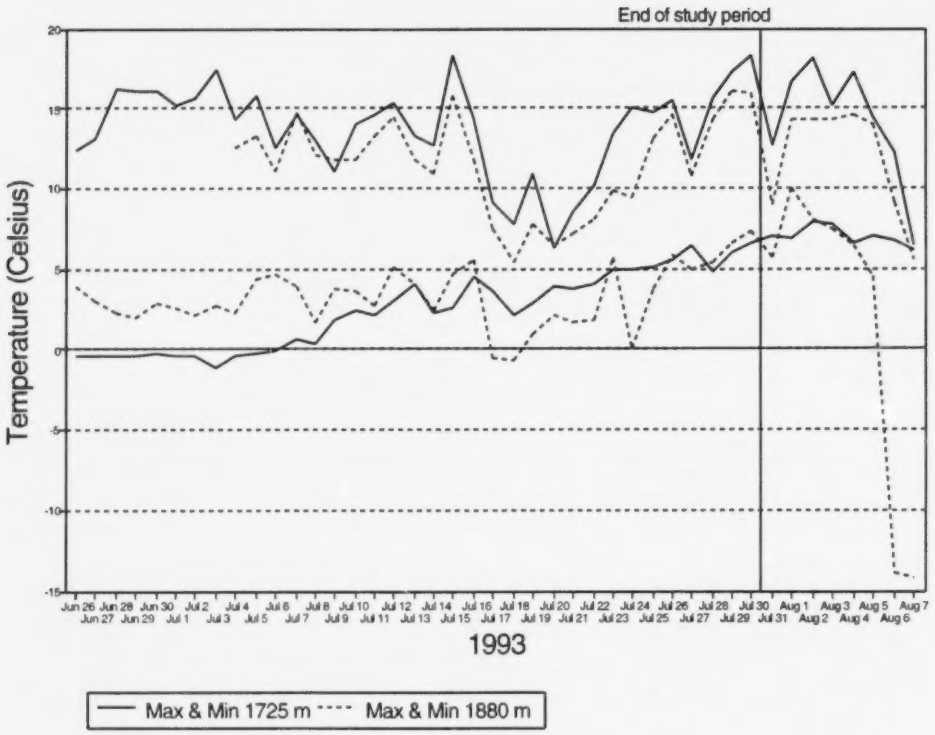
End of study period
Temperature (Celsius)
20
15
10
5
0
-5
-10
-15
Jun 26 Jun 27 Jun 28 Jun 29 Jun 30 Jul 1 Jul 2 Jul 3 Jul 4 Jul 5 Jul 6 Jul 7 Jul 8 Jul 9 Jul 10 Jul 11 Jul 12 Jul 13 Jul 14 Jul 15 Jul 16 Jul 17 Jul 18 Jul 19 Jul 20 Jul 21 Jul 22 Jul 23 Jul 24 Jul 25 Jul 26 Jul 27 Jul 28 Jul 29 Jul 30 Jul 31 Aug 1 Aug 2 Aug 3 Aug 4 Aug 5 Aug 6 Aug 7
1993
Max & Min 1725 m
Max & Min 1880 m

Figure 3.7. Daily temperature minima and maxima recorded by datalogger at elevations of 1725 m and 1880 m, 26 June to 1 August 1993.

*Relationships*

Five strong, significant relationships were discovered between meteorological, activity and harassment variables, all of which involved correlations between 0.652 and 0.739 in strength (Table 3.7). Air temperature was involved in the three of these five relationships.

Table 3.7. Summary of Pearson correlation matrix. Only significant relationships with r-values greater than 0.6 are shown from a pool of meteorological, activity, and harassment variables. Observations were collected between 26 June and 1 August 1993.

| Variable 1 | Variable 2 | r |
|---|---|---|
| Air temperature | % of time standing | + 0.727 |
| Air temperature | % of time feeding | - 0.652 |
| Air temperature | Distance to snowpatch | - 0.715 |
| Distance to snowpatch | % of time feeding | + 0.729 |
| Windspeed | Harassment | + 0.739 |

## Discussion

At northern latitudes, ungulate activity in summer is generally characterized by foraging activity peaks at sunrise and sunset, a pattern associated with diurnal changes in the thermal environment and insect avoidance (White *et al.* 1975, Gates 1980, Ion & Kershaw 1989, Russell *et al.* 1992). Caribou exhibited a circadian activity pattern of feeding and travelling in the morning, and resting and standing in the afternoon (Fig. 3.1a, 3.1b, 3.2a, 3.2b). Air temperature, which was strongly positively correlated with insect activity in the literature (Roby 1978, Helle & Tarvainen 1984), also had a strong relationship with both percent of time standing and feeding ($r=0.727$, $p=0.000$; $r=-0.652$, $p=0.000$). As the temperature increased (Fig. 3.6), caribou abandoned feeding and sought snowpatches on which to stand or lie (Fig. 3.1a, 3.1b, 3.2a, 3.2b), presumably to escape flying insects (Ion & Kershaw 1989). Caribou were less likely to feed as they got closer to a snowpatch, a hypothesis validated by the positive relationship between distance to a snowpatch and percent of time feeding ($r=0.729$, $p=0.000$). It should be noted that vegetation appears to decrease in both cover and diversity as one approaches snowpatches, making snowpatch areas inappropriate for efficient feeding.

Sexual differences in summer activity and habitat use have been reported for caribou (Roby 1978, Helle 1980, Whitten & Cameron 1986, Jakimchuk *et al.* 1987). Males and females differed significantly in their activities throughout most of the day (Table 3.2) with males spending less time standing and more time lying than females (Fig. 3.1a, 3.1b). As standing is a behaviour associated with insect harassment (Roby 1978, Downes *et al.* 1986, Russell *et al.* 1992), the frequent observation of standing female caribou could imply a sexually-determined intolerance to insects on the part of females. However, this makes little intuitive sense given the obvious vulnerability of the velvet-covered antlers of a bull caribou to blood-sucking insects. In addition, males were observed in a state of harassment at a greater frequency than were females (Fig. 3.3), and there was no significant difference between the sexes in distance to snowpatches (relief habitat) from late morning to evening, when insects were most active (Table 3.4).

A possible explanation involves the social habits of each sex and how these may affect insect harassment during the fly season. The majority of females sighted were members of post-calving aggregations of up to 150 animals while males were often solitary or in smaller groups of two or three individuals. Bergerud (1984) suggests that post-calving aggregations offer cows with vulnerable calves a defense against predators. The formation of large nursery bands may be initiated in an attempt to avoid predation of calves, despite the consequent production of more carbon-dioxide and warm convection currents

which may act as homing signals for mosquitoes (Roby 1978). Within these group situations, it is likely advantageous, in terms of insect avoidance, to stand. As an illustration, the mingling behaviour of a group of females standing on a snowpatch may be disruptive to flying insects (Roby 1978), and may also lead to a 'sharing' of the area at the center of the group, where harassment is believed to be minimized (Helle & Aspi 1983).

In contrast, male caribou which were frequently seen alone or in small groups appeared to lie down for much of the afternoon, as there was apparently no advantage to standing. However, in the late afternoon when temperatures and harassment were both at their daily peak (Fig. 3.3, 3.6), male caribou were frequently seen standing, possibly to allow themselves the mobility to discourage insect attackers with stamping, bucking, running, and other behaviours. The standing activity of male caribou in the late afternoon may also indicate the presence of oestrid flies which are known to elicit aggressive avoidance behaviours (Thomas & Kiliaan 1990). Late afternoon was the only time of day when the activities participated in by males and females did not differ significantly (Table 3.2). Perhaps in the late afternoon, insect avoidance became the sole determinant of behaviour.

With regard to insect avoidance, peaks of harassment behaviour occurred in the late morning and late afternoon (Fig. 3.3). This was also when dramatic changes were taking place in the average distance of a caribou to a snowpatch because the animals were moving on and off of the snow (Fig. 3.4). Thus, the first harassment peak may be the cue that drove the caribou onto the snow in search of relief, while the second peak may mark the period between leaving the snowpatch to feed and the eventual ceasing of insect activity in the evening. The minimal harassment during the afternoon would suggest that the use of relief habitat was an effective means of evading insects (Downes *et al.* 1986). With this in mind, the absence of a harassment comparison between the first and second half of the season may be inconsequential. Assuming that caribou are capable of evading insects through the use of relief habitat, a more appropriate measure of the change in insect-avoidance over the summer might be the distance from an animal to the nearest snowpatch. This did not change during the warmest period of the day (1500 - 1899 h) but decreased significantly during the late morning and evening, implying a greater duration of use of relief habitat (Table 3.5).

Downes *et al.* (1986) suggested that caribou can easily elude mosquitos through their altitudinal movements, and that avoidance behavior, such as head-shaking and bucking, is primarily the result of oestrids. If this is the case, the intense harassment in the late afternoon may also be the result of warm temperatures and coincident oestrid activity, a belief supported by the frequent observation of caribou in the "insect stance" associated with avoidance of bot flies. A significant change in activity budgeting occurred in the latter half of the fly-season, a time usually associated with oestrid and fly activity (Table 3.2). After 15 July, activity was characterized by standing (Fig. 3.2b), an observation consistent with research findings at other localities (Roby 1978, Downes *et al.* 1986).

With regard to changes in group size, however, this study contradicts Downes *et al.* (1986) who described an increase in group size throughout the first half of the fly season until the appearance of oestrids, at which time caribou dispersed into smaller groups. In this study, group size between 1100 and 2300 h increased significantly throughout the season (Table 3.6). Prior to 15 July, late morning and afternoon were characterized by dispersal while following 15 July, there was a dramatic change in daily patterns with the smallest groups appearing in the morning and evening and the largest in the afternoon (Fig. 3.6). This change in group size is likely related to a change in insect activity.

Subjectively speaking, there was a definite increase in the abundance of insects over the summer, likely related to the increase in minimum temperature at lower elevations (Fig. 3.7), and this probably led to aggregation behaviours adopted by caribou to "swamp" attacking insects. Although such behavior may not always be indicative of late summer, in the study area aggregation may be an appropriate response to any insect harassment, regardless of whether it is precipitated by mosquitos or oestrids, because relief habitat is

discrete and in limited supply (Bergerud 1974, Jakimchuk *et al.* 1987). This became obvious toward the end of the fly-season when many of the late-lying snowpatches began to disappear through melt. In addition, besides overwhelming the attackers, aggregation provides security for the individuals at the center of the group, possibly even in the presence of warble or bot flies (Bergerud 1974).

Finally, the positive correlation between windspeed and harassment ($r=0.739$, $P=0.000$) was not expected, as mosquitos were not expected to fly well in the wind. Both temperature and windspeed reached their peaks at approximately the same time of day (Fig. 3.6), and it is possible that high temperatures increased the tolerance of mosquitos for wind. Regarding this theory, the average daily peak temperature in the study area was approximately 9 °C associated with an average daily peak wind of approximately 3.2 $ms^{-1}$. White *et al.* believed that moderate harassment would occur at air temperatures of 9 °C with windspeeds up to 6 $ms^{-1}$. Similarly, Russell *et al.* (1993) postulated that mosquito activity would not diminish until windspeeds exceeded 4.4 $ms^{-1}$ and would cease at approximately 6 $ms^{-1}$. Thus, it is possible that windspeed seldom maintained sufficient magnitude to discourage mosquito activity.

However, even if windspeed did exceed tolerable levels for mosquitos, it may not have impeded the flight of oestrids. These large flies are less affected by wind, and may have been responsible for harassment of caribou late in the day as they require a higher temperature to initiate flight. Moreover, the late afternoon timing of oestrids taking wing may actually be coincident with anabatic wind events. Anabatic winds occur in the afternoon when the entire air mass of a valley is heated up and begins an up-valley movement, (Janz & Storr 1977, Oke 1978). Upslope winds may also serve to move insects into areas above their wetland breeding sites in valley bottoms.

## Conclusions

1. Caribou displayed circadian activity cycles between 0700 and 2300 h, whereby they fed and travelled in the early morning and late evening, and spent the afternoons lying down and standing. This pattern was coincident with daily temperature cycles and was likely a means of insect avoidance. Activity budgets changed significantly over the course of the study, with caribou spending more time standing in the latter half, probably as a result of increased insect activity.
2. Female and male caribou displayed significant differences in activity budgets between 0700 and 1459, and 1900 and 2300 h. Between 1500 and 1859 h, both sexes were similar in their activities, possibly due to the overriding influence of insect activity in the late afternoon. Female caribou spent more time standing than did males. Standing may be advantageous to females,which were frequently seen in large post-calving aggregations, as opposed to males, which were generally alone or in small groups.
3. Both male and female caribou displayed circadian habits in their use of snowpatch relief habitat, minimizing distance to snowpatches in the late morning and afternoon while increasing this distance at other times of day. Harassment by insects was greatest during the transition time when caribou were moving onto the snow, and in the late afternoon when daily temperature reached a peak. Activity of oestrid flies may also have contributed late afternoon harassment. During the second half of the season, when insects presumably became more abundant, mean distance to a snowpatch in the late morning and early afternoon decreased significantly.
4. Caribou exhibited a significant increase in group size in the latter half of the study, forming large aggregations in the early afternoon in late summer. This was believed to be the result of increased insect harassment and decreased availability of late-lying snowpatches due to a general warming trend throughout the season.

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# Circadian patterns in summer microhabitat selection by mountain caribou.

## Introduction

Comprehensive studies of summer habitat use by mountain caribou have tended to focus on seasonal patterns. Stelfox *et al.* (1978) conducted detailed, and somewhat site-specific, summer habitat research as part of a larger seasonal study in Jasper National Park while Bloomfield (1980) included summer range in a year-long study which examined seasonal habitat use in the Selkirk mountains, B.C. Finally, Oosenbrug and Theberge (1986) studied vegetation and topographic preferences of caribou in the Kluane Ranges, Y.T. on a monthly basis throughout two summers.

More specifically, comprehensive work on circadian habitat patterns is essentially nonexistent. Numerous papers have made anecdotal references to the predictable daily movement patterns of *Rangifer* (Banfield 1954, Kelsall 1968, White *et al.* 1975, Helle 1980, Skogland 1980, Bergerud 1974, Downes *et al.* 1986), but few have attempted to study these observations in detail. Some studies have examined specific circadian rhythms, for example, both Roby (1978) and Russell *et al.* (1993) wrote of diurnal activity patterns, and Ion and Kershaw (1989) examined daily use of snowpatch relief habitat; however, no one has published results concerning the diurnal selection of habitat in any broader sense.

Researchers have attempted to identify specific ecological components which influence habitat selection. One important factor appears to be forage. Researchers agree that caribou will select foraging sites based on the quantity and quality of vegetation available (White *et al.* 1975, Bergerud 1978, Skogland 1980, Servheen & Lyon 1989). However, the selection between available feeding sites is believed to be influenced by other factors, including the abundance and activity of flying insects (White *et al.* 1975, Roby 1978, Downes *et al.* 1986, Ion & Kershaw 1989, Russell *et al.* 1993), and the likelihood of encountering predators (Bergerud *et al.* 1984, Bergerud & Page 1987, Jakimchuk *et al.* 1986, Seip 1992). Although the first habitat priority for a caribou may be forage abundance and quality, this is apparently constrained by an aversion to both insects and predators. In addition, other factors, such as temperature and the presence of other ungulate species may be important. In light of this, caribou must temporally partition their use of habitat to meet their specific needs.

The study of temporal habitat partitioning can serve as a basis for clarifying a caribou's ecological needs and priorities. By recording the instantaneous positions of an individual woodland caribou within its habitat, researchers capture "frozen moments" in the continuous and dynamic spatial process whereby an animal continuously prioritizes its habitat requirements and adjusts its position accordingly. Each position represents the end product of an animal's interaction with its environment, and its consequent spatial adaptation. By collecting these 'frozen moments' and putting them in the context of the relevant literature, this study examines habitat prioritization as expressed in the diurnal habitat selection patterns of summering mountain caribou in the Mackenzie Mountains, N.W.T.

## Study area

Macmillan Pass is an east/west running corridor which transects the Mackenzie/Selwyn mountains. The study area, located 15 km east of the Pass, is utilized by caribou from the Redstone herd from June until late September (Miller 1976, Urquhart & Urquhart 1977, Farnell & Nette 1981). It covers an area of approximately 14 $km^2$, all above timber-line, and extends south of the CANOL road over flat, rolling tundra, up the side of a mountainous dome, and down into the valley beyond. Six basic habitat associations were identified within the study area: snowpatch/bare rock, alpine lichen-grass, lichen-heath, mesic meadow, forb meadow, and birch/willow associations.

In the center of the study area, a summit dome, at 1970 m ASL, provided a high altitude plateau approximately 200 m across, covered partially with patterned circles of

cobbles, and with an alpine lichen-grass community, characterized by a thin, sporadic covering of lichens (*Cetratria* spp., *Cladina mitis*) and alpine grasses (*Deschampsia caespitosa*, *Festuca altaica*, *Poa arctica*). The sides of the dome were very steep in all directions, particularly to the west where the slope was dominated by a precipitous, high-angled scree slope. To the south was a rocky saddle which descended back to the headwaters of an unnamed river, and beyond to the snowy faces of two mountains, each exceeding 2000 m ASL.

Descending the dome to the east involved traversing late-lying snowpatches and steep slopes of rock, apparently shattered *in situ*. As the slope became more moderate, patches of lichen-heath (*Cladina mitis, Cassiope tetragona*) dominated communities appeared. These formed a near continuous cover over the landscape which was transected only by small rivulets, fringed in bands of forb meadow, draining snowmelt water down to a tributary valley, 400 m below. Farther downslope, the lichen-heath became patchy, confined to the north-facing slopes of hummocks, and interspersed with areas of graminoid-dominated, mesic meadow (*Deschampsia caespitosa*, *Carex podocarpa*, *Festuca altaica*) on raised areas and ridges. All water courses and moist depressional areas were characterized by rich forb meadows (*Carex* spp., *Senecio triangularis, Salix arctica, S. reticulata*, numerous forbs), occasionally interrupted by sporadic thickets of willow (*Salix* spp.).

On the north face of the summit dome, large late-lying snowpatches which were several meters deep in early July, persisted throughout the summer. Meltwater from these drained down to an expansive plateau below. At 1725 m ASL, the meltwater run-off sustained a vegetation mosaic consisting of forb meadows in depressions and drainages, and lichen-heath and mesic meadows on ridges and hummocks. Beyond this plateau, the mountain slope dropped swiftly down through lichen-heath communities, abundant in "reindeer lichens" (*Cladina mitis, C. rangiferina*).

At approximately 1500 m ASL, the terrain levelled out and shrubs dominated the landscape down to the floor of the Pass (1300 m). Birch (*Betula glandulosa*) appeared on drier sites, accompanied by lichens (*Cladina mitis, C. rangiferina*) or mosses depending on the moisture regime. Willow (*Salix lanata, S. glauca, S. planifolia, S. reticulata*) appeared in riparian areas in association with mosses, and around two wetland-bordered lakes at the base of the study mountain with an understory of forbs and sedges (including *Artemesia tilesii*, *Mertensia paniculata*, *Petasities frigida, Carex aquatilis*). Small grassy meadows were infrequently scattered throughout the birch-lichen communities which covered the majority of the bottom of the Tsichu River valley.

## Methods

*Habitat use*

Habitat use was assessed primarily through focal sampling (Altmann 1974) of wild caribou between 26 June and 1 August 1993. Researchers hiked a belt transect from the valley floor to the summit dome of an unnamed mountain, stopping at set locations to search for caribou with binoculars. Eventually a mountain camp was established at 1680 m ASL to facilitated surveys at high altitudes; however, observers frequently conducted searches of lower elevations, both with a spotting scope and during hikes to and from the alpine camp.

At the start of each survey, the landscape was searched using binoculars. The first caribou spotted was used as the subject of focal observation. Frequently, it was possible to include more than one individual in observations due to the high visibility of the tundra-dominated landscape and the grouping behaviour of caribou (particularly toward the end of the study). Observations of focal animals were continued for as long as possible.

Although all subject animals were continuously monitored, focal observations were divided into ten minute blocks to better facilitate data management. The amount of time each caribou spent in different habitat associations was recorded, as was its location in terms of slope, elevation, and aspect.

Analyses of variance (ANOVA) (Wilkinson 1988) were conducted to investigate whether the sex of a caribou influenced its use of slope or elevation at various times of day. ANOVA was also used to determine if the use of slopes and elevations at various times of day changed significantly throughout the study.

Hourly use of habitat was determined based of the frequency with which animals were observed in different plant communities during different periods of the day. Chi-squared tests (Sokal & Rohlf 1981) were used to determine if habitat use differed significantly between male and female caribou throughout the day. Chi squared tests were also used to test for a possible change in the use of vegetated and unvegetated habitats from the first to the second half of the season.

*Habitat availability*

Because aerial photography of the entire study area was not available, a more creative methodology was necessary to estimate the area occupied by each plant community. Viewsheds (the area visible from a lookout) were estimated for points along the belt transect using a 1:50,000 contour map. This provided an estimate of the size of the entire area that was surveyed for caribou. The total survey area was then subdivided into seven, ecologically-similar polygons. Using what aerial photography was available, in combination with personal photographs, memories, testimony of field personel, and a small scale vegetation map (Kershaw & Kershaw 1983), the percent coverage of the dominant habitat associations within each smaller polygon was estimated. A planimeter was then used to measure the area of the seven polygons and this formed the basis for percent cover calculations of habitat associations for the entire study area.

*Habitat selection*

A number of mathematically-sophisticated techniques are available for determining the selectivity of a species for a habitat; however, the observational data collected in the field did not lend itself well to any of these. As observations were broken down into ten-minute blocks and then combined into categories, use of techniques that rely on comparison of one animal to another was not possible (Johnson 1980, Byers *et al* 1984, Aebischer *et al*.1993). In addition, the inability of such statistical techniques to cope with situations where habitat use equals zero rendered them inappropriate for diurnal investigation where certain habitat associations were only utilized at certain times of day. Because of this, a comparatively simple method of calculating selection was used.

Selectivity was determined for two hour periods between 0700 and 2300 hours. The relative selectivity of each habitat association was calculated using a simple formula adapted from Russell *et al* (1993) which produces a value indicative of both the direction and strength of selection.

$$S_{ik} = (U_{ik}-A_i)/(U_{ik}+A_i)$$

where: $S_{ik}$=relative selectivity for plant community i at time k
$U_{ik}$=percent use of plant community i at time k.
$A_i$=percent availability of plant community i.

*Presence of predators/alternate prey species*

The presence of predators was crudely monitored throughout the study by noting the occurrence of wolverines, wolves, grizzly bears, golden eagles, or their sign when encountered. In addition, the presence of any alternate prey species, such as moose, marmots, ground squirrels, lemmings, pika, and ptarmigan, was also recorded.

*Meteorological conditions and insect-harassment response*

Temperature and windspeed were measured using hand-held instruments, at ten minute intervals while animals were under observation. Cloud cover was also estimated.

Two automated data loggers were also utilized - one recording temperature and windspeed located adjacent to a snowpatch at 1880 m ASL, and the other recording only temperature in a forb meadow at 1725 m. Data were automatically averaged over two hour intervals.

Data concerning responses of caribou to insect harassment were collected in the manner described in the previous paper.

## Results

*Use of aspects*

Cool, northeastern aspects (0 - 89°) were used most often throughout the day (Fig. 4.1). In general, most variation from the northeastern aspects occurred in the morning and the evening. Female caribou used northeastern aspects exclusively between 1100 and 1700 hours, but occupied other aspects during the morning and the evening hours, favoring those to the southeast. Males used both southeastern and northwestern aspects in the morning, but tended to utilize primarily northeastern slopes the rest of the day.

*Use of slopes*

In general, the angle of slopes that were utilized tended to increase toward afternoon for both males and females (Fig. 4.2); however, females utilized significantly steeper slopes than males for the majority of the day (Table 4.1). The angle of slopes utilized increased significantly over the study from 0700 in the morning until 1900 in the evening (Table 4.2).

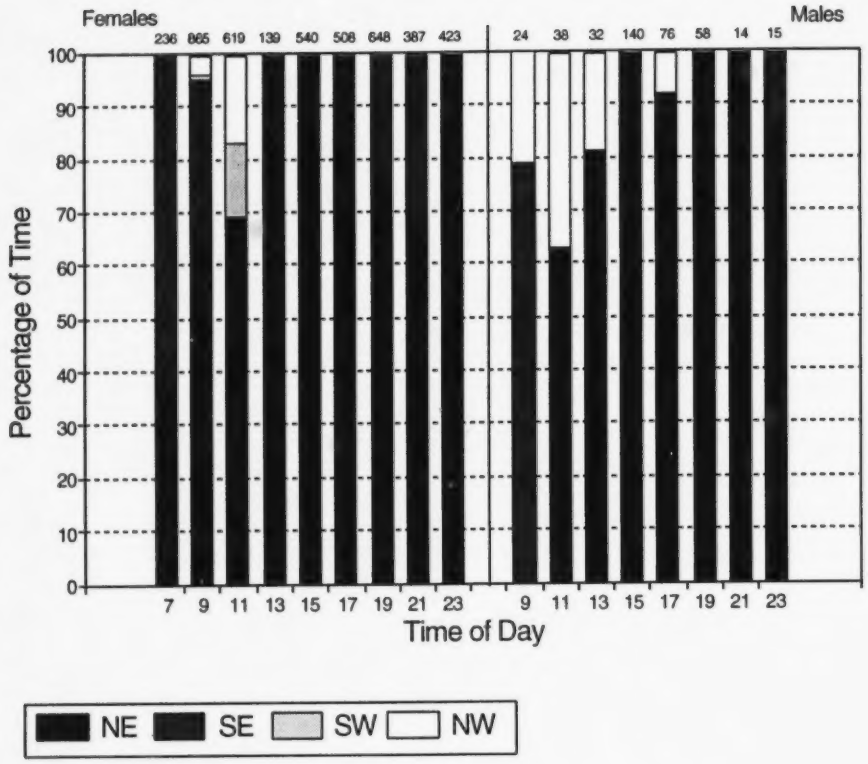


Figure 4.1. Aspects utilized by male and female caribou between 26 June and 1 August 1993. Each numeral on the time of day scale represents observations for the two previous hours. Annotated numbers are sample size.

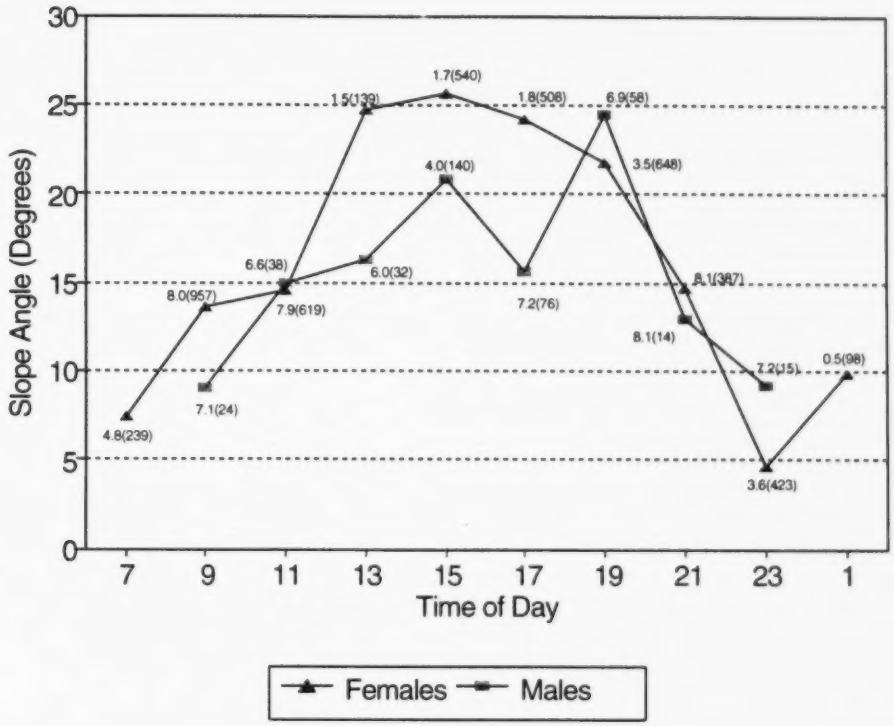


Figure 4.2. Mean slope angles utilized by male and female caribou between 26 June and 1 August 1993. Each numeral on the time of day scale represents observations for the two previous hours. Annotated numbers are standard deviations with sample size in parentheses.

Table 4.1. Summary of ANOVA based on the slopes utilized by male and female caribou at different times of day. Observations were collected between 26 June and 1 August 1993.

| Time Period | Sex | Mean Slope | SD | n | F-ratio | p | $H_0$ ? |
|---|---|---|---|---|---|---|---|
| 0700-1059 | F | 14.0 | 8.0 | 1576 | | | |
| | M | 12.7 | 7.4 | 62 | 1.491 | 0.222 | Accept $H_0$ |
| 1100-1459 | F | 25.4 | 1.7 | 679 | | | |
| | M | 20.0 | 4.7 | 172 | 603.781 | 0.000 | Reject $H_0$ |
| 1500-1859 | F | 22.9 | 3.1 | 1156 | | | |
| | M | 19.5 | 8.3 | 134 | 87.637 | 0.000 | Reject $H_0$ |
| 1900-2300 | F | 9.4 | 8.0 | 810 | | | |
| | M | 11.0 | 7.8 | 29 | 1.119 | 0.000 | Reject $H_0$ |

SD: standard deviation.
n: number of observations.
p: probability that $H_0$ is true.
$H_0$: there is no significant difference between the use of slopes by male and female caribou.

Table 4.2. Summary of ANOVA based on use of slopes at different times of day throughout the season. Observations were collected between 26 June and 1 August 1993.

| Time Period | Half | Mean Slope | SD | n | F-ratio | p | $H_0$ ? |
|---|---|---|---|---|---|---|---|
| 0700-1059 | 1 | 18.1 | 6.9 | 1693 | | | |
| | 2 | 10.9 | 7.7 | 1120 | 659.248 | 0.000 | Reject $H_0$ |
| 1100-1459 | 1 | 18.5 | 3.6 | 149 | | | |
| | 2 | 25.1 | 1.0 | 3557 | 4167.366 | 0.000 | Reject $H_0$ |
| 1500-1859 | 1 | 11.7 | 4.6 | 65 | | | |
| | 2 | 23.4 | 3.1 | 2057 | 844.863 | 0.000 | Reject $H_0$ |
| 1900-2300 | 1 | 9.6 | 6.6 | 10 | | | |
| | 2 | 9.3 | 7.9 | 1125 | 0.007 | 0.993 | Accept $H_0$ |

Half 1: 26 June - 15 July 1993
Half 2: 16 July - 1 August 1993
SD: standard deviation
n: number of observations.
p: probability that $H_0$ is true.
$H_0$: there is no significant difference between the use of slopes by caribou during the first half and the last half of the season.

*Use of elevations*

Elevation use throughout the day followed a convex curve in which extreme elevations were used at midday (Figure 4.3). Females and males utilized similar elevations in the early morning and late evening, but cows were seen at significantly higher elevations in late morning and afternoon (Table 4.3). Caribou occupied significantly higher elevations at all times of the day in the latter half of the season relative to the first half (Table 4.4)

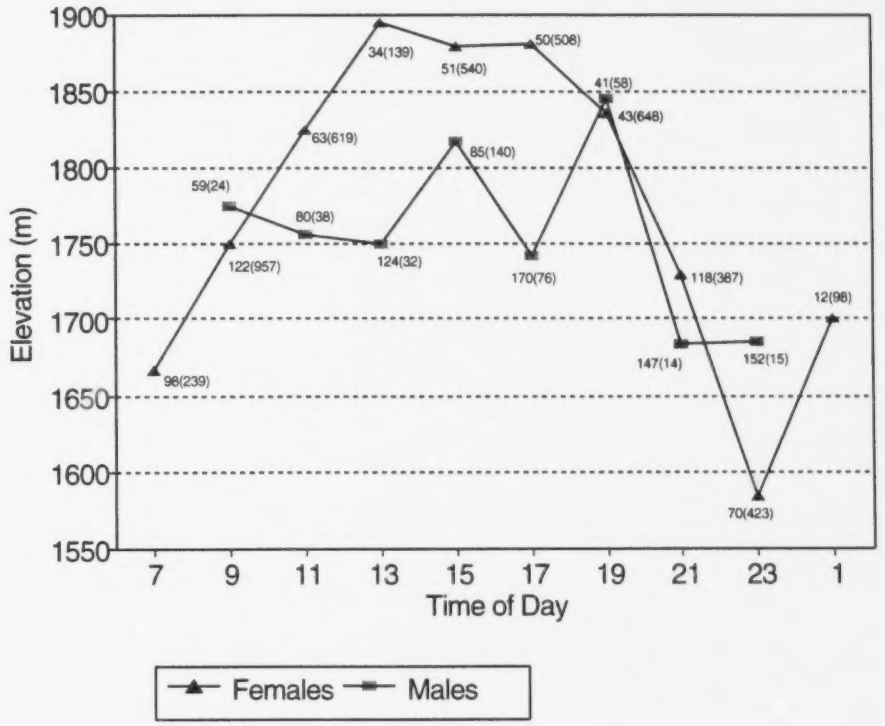


Figure 4.3. Mean elevations utilized by male and female caribou between 26 June and 1 August 1993. Each numeral on the time of day scale represents observations for the two previous hours. Annotated numbers are standard deviations with sample size in parentheses.

Table 4.3. Summary of ANOVA based on the elevations utilized by male and female caribou at different times of day. Observations were collected between 26 June and 1 August.

| Time Period | Sex | Mean Elevation | SD | n | F-ratio | p | $H_0$ ? |
|---|---|---|---|---|---|---|---|
| 0700-1059 | F | 1779 | 109 | 1576 | | | |
| | M | 1763 | 73 | 62 | 1.293 | 0.256 | Accept $H_0$ |
| 1100-1459 | F | 1882 | 49 | 679 | | | |
| | M | 1804 | 97 | 172 | 218.085 | 0.000 | Reject $H_0$ |
| 1500-1859 | F | 1855 | 51 | 1156 | | | |
| | M | 1786 | 140 | 134 | 131.531 | 0.000 | Reject $H_0$ |
| 1900-2300 | F | 1653 | 120 | 810 | | | |
| | M | 1684 | 147 | 29 | 1.841 | 0.175 | Accept $H_0$ |

SD: standard deviation.
n: number of observations.
p: probability that $H_0$ is true.
$H_0$: there is no significant difference between the elevations utilized by male and female caribou.

Table 4.4. Summary of ANOVA based on the use of elevations at different times of day throughout the year. Observations were collected between 26 June and 1 August.

| Time Period | Half | Mean Elevation | SD | n | F-ratio | p | $H_0$ ? |
|---|---|---|---|---|---|---|---|
| 0700-1059 | 1 | 1790 | 97 | 1693 | | | |
| | 2 | 1771 | 111 | 1120 | 23.966 | 0.000 | Reject $H_0$ |
| 1100-1459 | 1 | 1777 | 71 | 149 | | | |
| | 2 | 1895 | 27 | 3557 | 2083.28 | 0.000 | Reject $H_0$ |
| 1500-1859 | 1 | 1657 | 157 | 65 | | | |
| | 2 | 1863 | 48 | 2057 | 568.945 | 0.000 | Reject $H_0$ |
| 1900-2300 | 1 | 1800 | 78 | 10 | | | |
| | 2 | 1651 | 120 | 1125 | 15.382 | 0.000 | Reject $H_0$ |

Half 1: 26 June - 15 July 1993
Half 2: 16 July - 1 August 1993
SD: standard deviation.
n: number of observations.
p: probability that $H_0$ is true.
$H_0$: there is no significant difference between use of elevations by caribou during the first half and the last half of the season.

*Use and selection of vegetation types*

The use of the six vegetation types varied significantly between males and females throughout the day (Table 4.5). Both sexes shared a near exclusive preference for barren areas at midday (Fig.4.4); however, they were more varied in their choice of preferential habitats at other times of day. Forb meadows were strongly selected by females in the morning and by both sexes in the evening (Fig. 4.5); in contrast, more mesic meadows were almost never selected (Fig. 4.6). Both sexes also selected alpine lichen-grass communities in the early hours (Fig. 4.7) and females also preferred these vegetation types, along with lichen-heath communities, in evening (Fig. 4.8). Willow- and birch-dominated

communities were never selected (Fig. 4.9). Over the season, caribou spent a significantly greater portion of their time in unvegetated habitats as opposed to well-vegetated habitats (Table 4.6).

Table 4.5. Frequency of use of vegetation types at different times of day by caribou, 26 June - 1 August 1993.

| Time period | Sex | MM | FM | LG | LH | W/B | NV | $Chi^2$ | DF | Alpha | $H^0$ ? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0700-1059 | F | 101 | 554 | 378 | 92 | 37 | 410 | | | | |
| | M | 6 | 5 | 22 | 4 | 0 | 23 | 21.8 | 5 | 0.05 | Reject $H^0$ |
| 1100-1459 | F | 0 | 0 | 0 | 2 | 0 | 675 | | | | |
| | M | 4 | 7 | 0 | 0 | 2 | 159 | 52.4[1] | 4 | 0.05 | Reject $H^0$ |
| 1500-1859 | F | 51 | 41 | 1 | 0 | 0 | 1063 | | | | |
| | M | 11 | 4 | 4 | 0 | 6 | 106 | 85.1[2] | 4 | 0.05 | Reject $H^0$ |
| 1900-2300 | F | 6 | 214 | 134 | 173 | 0 | 277 | | | | |
| | M | 2 | 13 | 1 | 2 | 1 | 10 | 48.0 | 5 | 0.05 | Reject $H^0$ |

[1]: LG omitted due to zeros. Low values or zeros in 1 out of 10 remaining cells.
[2]: LH omitted due to zeros. Low values or zeros in 6 out of 10 remaining cells.
MM: mesic meadow
FM: forb meadow
LG: alpine lichen and grass community
LH: lichen and bell-heather community
W/B: subalpine willow or birch dominated community
NV: unvegetated tundra (often snow covered)
DF: degrees of freedom
$H^0$: there is no significant difference between the use of vegetation types by male and female caribou.

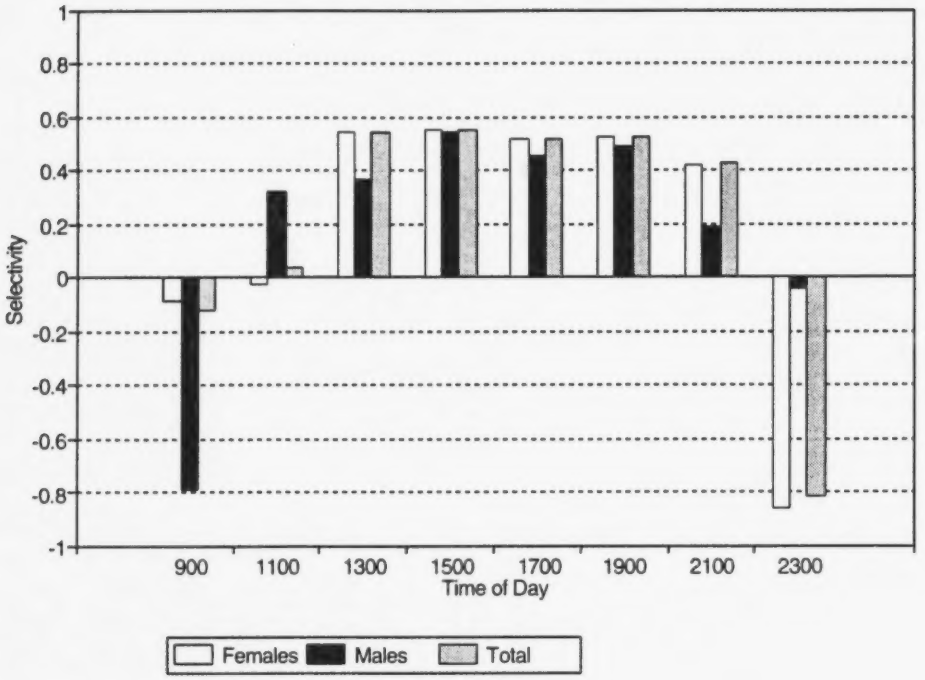


Figure 4.4. Selectivity of unvegetated habitats by male, female, and total caribou observed 26 June to 1 August 1993. Positive values indicate selection; negative values show avoidance. Each numeral on the time of day scale represents observations for the two previous hours.

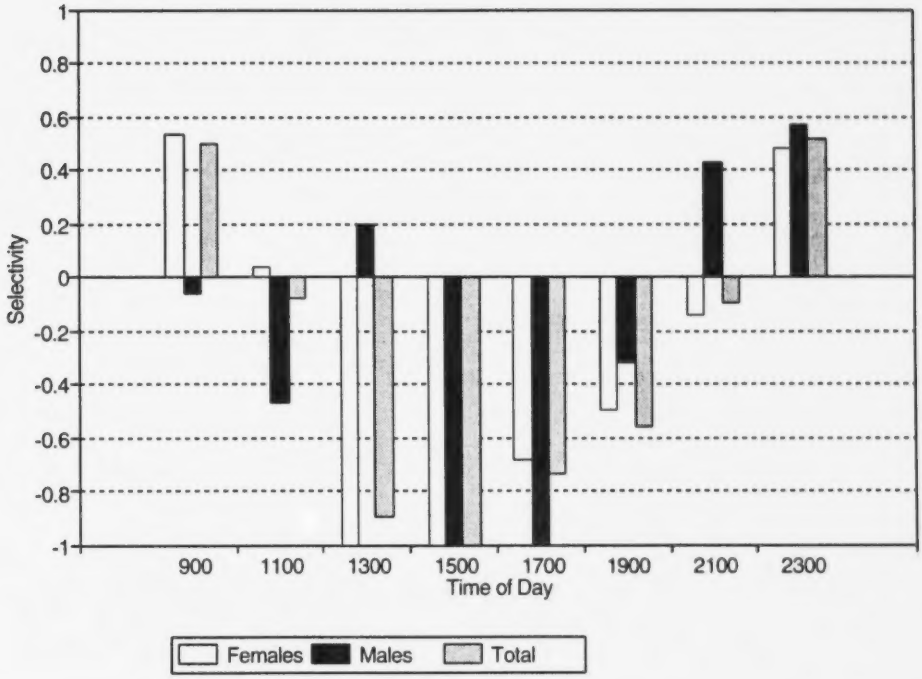


Figure 4.5. Selectivity of forb meadow vegetation types by male, female, and total caribou observed 26 June to 1 August 1993. Positive values indicate selection; negative values show avoidance. Each numeral on the time of day scale represents observations for the two previous hours.

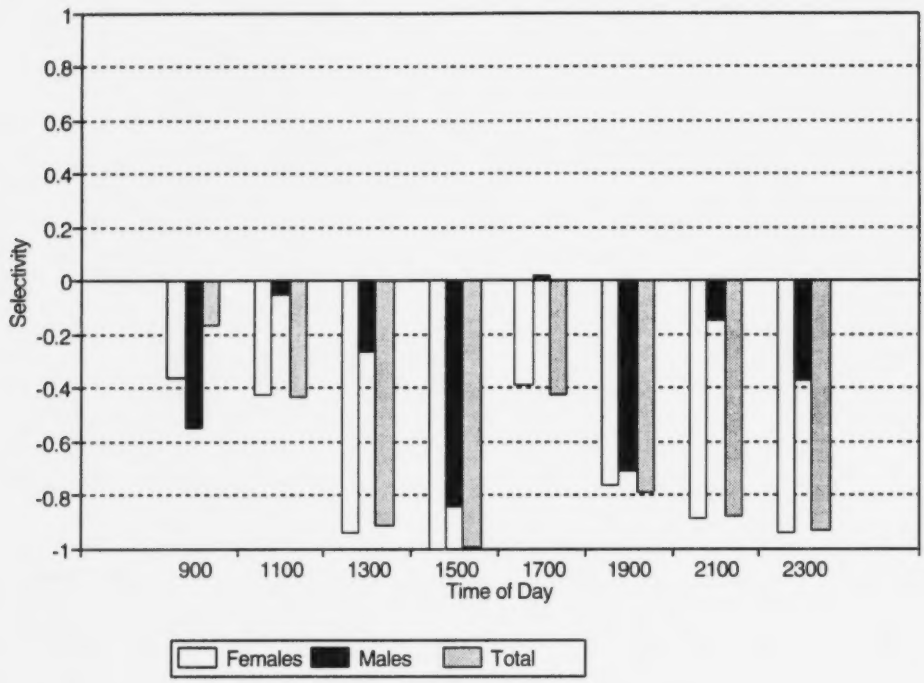


Figure 4.6. Selectivity of mesic meadow vegetation types by male, female, and total caribou observed 26 June to 1 August 1993. Positive values indicate selection; negative values show avoidance. Each numeral on the time of day scale represents observations for the two previous hours.

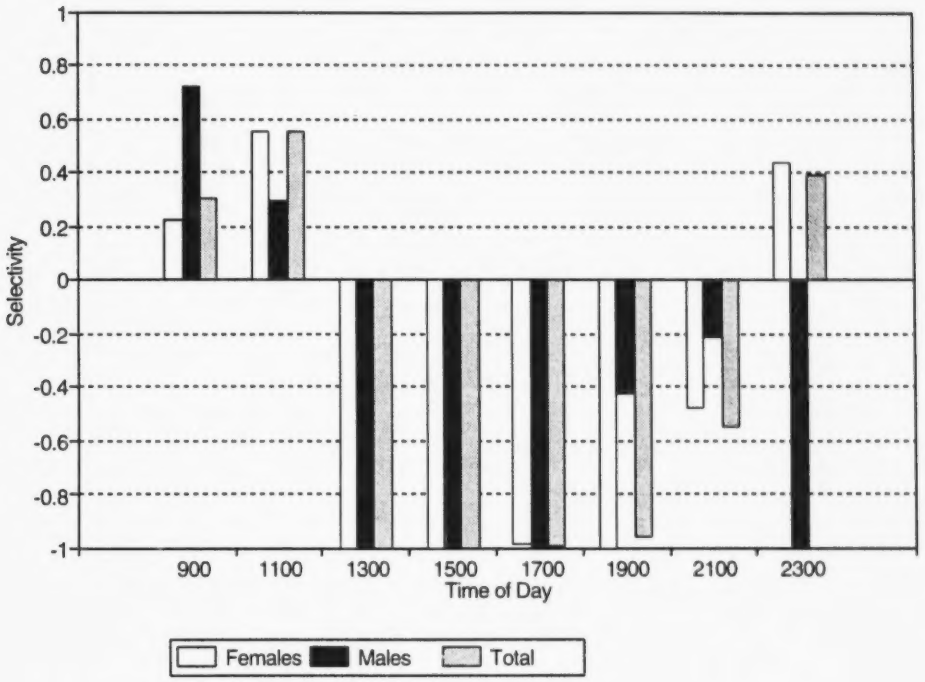


Figure 4.7. Selectivity of alpine lichen-grass vegetation types by male, female, and total caribou observed 26 June to 1 August 1993. Positive values indicate selection; negative values show avoidance. Each numeral on the time of day scale represents observations for the two previous hours.

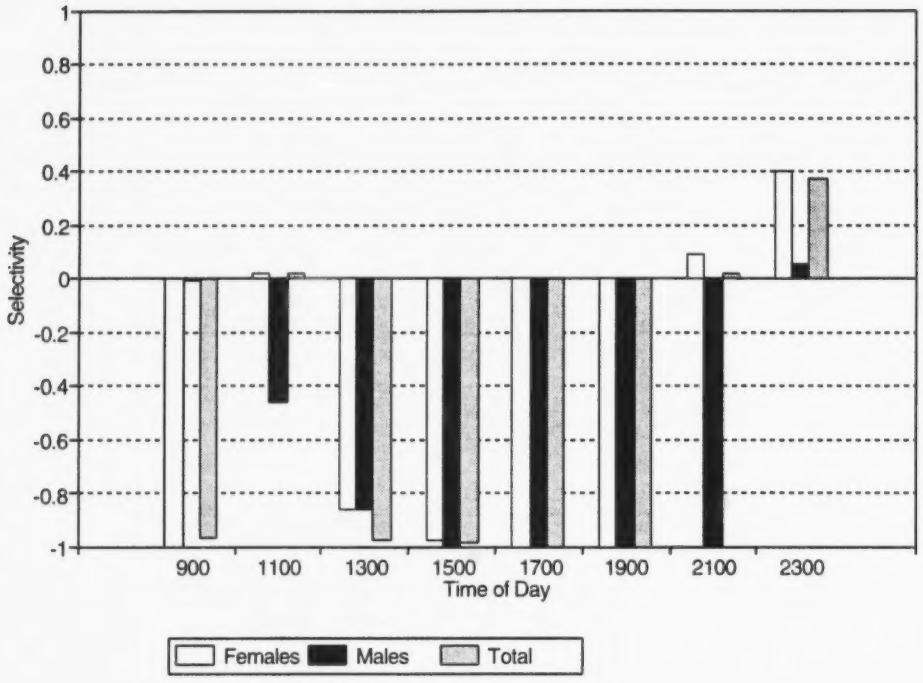


Figure 4.8. Selectivity of lichen-heath vegetation types by male, female, and total caribou observed 26 June to 1 August 1993. Positive values indicate selection; negative values show avoidance. Each numeral on the time of day scale represents observations for the two previous hours.

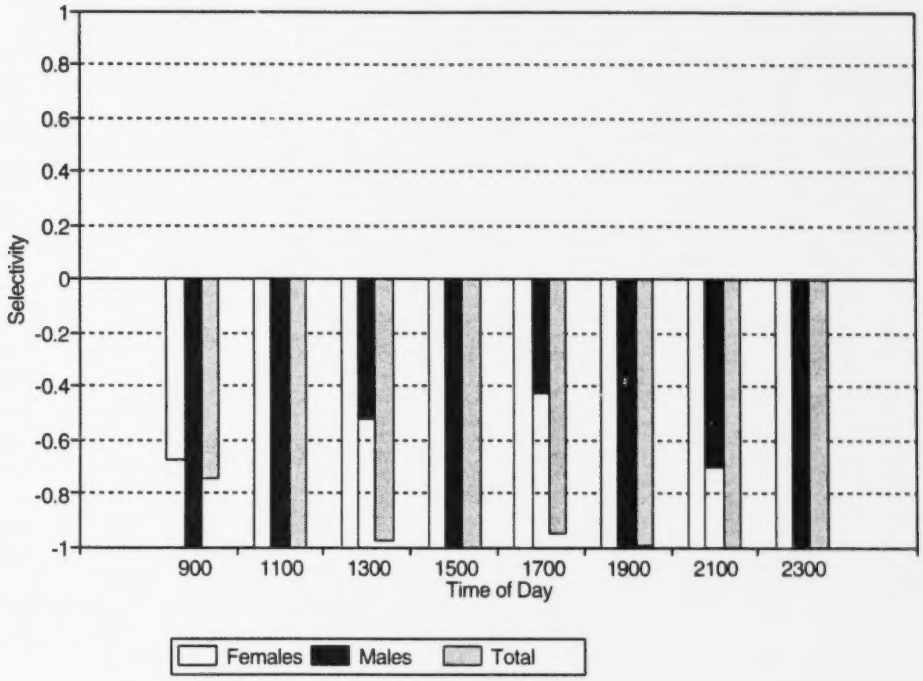


Figure 4.9. Selectivity of willow or birch shrub vegetation types by male, female, and total caribou observed 26 June to 1 August 1993. Positive values indicate selection; negative values show avoidance. Each numeral on the time of day scale represents observations for the two previous hours.

Table 4.6. Frequency of use of vegetated and unvegetated habitats by caribou, 26 June - 1 August, 1993.

| Time period | Half | NV | VG | $Chi^2$ | DF | Alpha | $H^0$ ? |
|---|---|---|---|---|---|---|---|
| 0700-1059 | 1 | 369 | 1324 | | | | |
| | 2 | 351 | 769 | 184.8 | 1 | 0.05 | Reject $H^0$ |
| 1100-1459 | 1 | 131 | 18 | | | | |
| | 2 | 3555 | 2 | 143.0 | 1 | 0.05 | Reject $H^0$ |
| 1500-1859 | 1 | 40 | 25 | | | | |
| | 2 | 1918 | 139 | 99.9 | 1 | 0.05 | Reject $H^0$ |
| 1900-2300 | 1 | 1 | 9 | | | | |
| | 2 | 393 | 732 | 29.1 | 1 | 0.05 | Reject $H^0$ |

Half 1: 26 June - 15 July 1993
Half 2: 16 July - 1 August 1993
NV: unvegetated areas
VG: vegetated areas
DF: degrees of freedom
$H_0$: there is no significant difference between caribou use of vegetated and unvegetated habitats during the first half and the last half of the season.

*Presence of predators/alternate prey species*

Within the study area, a variety of predators and alternate prey species were identified (Table 4.7). Grizzly bears were sighted frequently relative to other summers (G.P. Kershaw, pers. comm.).

Table 4.7. Predators and alternate prey species sighted in the study area, 26 June - 1 August 1993.

| Species | Evidence | Terrain (elevations ASL) | Plant Community |
|---|---|---|---|
| Wolf | 2 Scat | Steep, northern slope @ 1650 m | Lichen-heath |
| | 2 Sighted | Summit dome @ 1880 m | Bare/snow |
| Grizzly Bear | 1 Scat | Riparian area @ 1350 m | Birch, willow-moss |
| | 5 Sighted | 2 - Alpine creek bed @ 1750 m | Forb meadow |
| | | 1 - Summit dome @ 1800 m | Bare/snow |
| | | 1 - Alpine plateau @ 1680 m | Lichen-heath |
| | | 1 - Base camp on valley floor @ 1300 m | Birch-lichen |
| Golden eagle | 4 Sighted | Circling over summit dome (1900 m) | Lichen-grass; bare |
| Moose | Many tracks | Moist, lakeside areas @ 1400 m | Willow-forb |
| | 2 Sighted | 1 - Riparian area @ 1300 m | Willow, birch-moss |
| | | 1 - Moist lakeside area @ 1400 m | Willow-forb |
| Marmot | Many sighted | Alpine valleys @ 1650 m | Alpine/forb meadow |
| Pika | Many sighted | Scree slopes @ 1750 m | Bare |
| Gr. Squirrel | Many sighted | Varied; 1300 - 1750 m | Varied |
| Ptarmigan | Many sighted | Varied; 1300 - 1750 m | Varied |

*Meteorological conditions and insect-harassment response*

Throughout the day, temperature and windspeed changed in a distinct pattern (Fig 3.6), both increasing throughout the morning, leveling off in the late afternoon, and decreasing into the evening. Windspeed appears to lag behind temperature.

Throughout the study period, maximum and minimum temperature at 1880 m ASL within the study area appeared to follow a consistently flat trend (Fig 3.7). Minimum temperature at 1725 m ASL, however, increased throughout the month of July even though maximum temperature at the same elevation did not have a similar upward trend.

Diurnal insect harassment of caribou appears somewhat bimodal in character, with two peaks, one in the late morning (0900 - 1059) and one in the early evening (1700 - 1859) (Fig. 3.3). The initial peak appeared to be coincident with the movement of caribou onto late-lying snowpatches (relief habitat) whereas the second peak appeared to occur as the animals moved off of the snow (Fig. 3.4).

*Relationships*

A Pearson correlation matrix was generated using the following variables which were collected during focal observations:

1. Elevation
2. Slope
3. Aspect
4. Temperature
5. Windspeed
6. Cloud cover

Strong, significant correlations occurred between temperature and elevation, and temperature and slope (r=0.685, p=0.000, and r=0.762, p=0.000 respectively).

## Discussion

Caribou are known to make directed and purposeful daily movements. White *et al.* (1975) stated that caribou avoided prime feeding sites at certain times of day when mosquitos were troublesome. Roby (1978) noted cyclic patterns in daily feeding and lying activities and Russell *et al.* (1993), upon witnessing similar patterns, speculated that the increased movement of caribou in the evening hours was due to travel from insect relief areas to feeding sights. Ion (1986) noted the late afternoon movement of caribou from snowpatch relief habitat near 2000 m ASL down to valley bottoms at 1700 m in the evenings. Within this study, observations were repeatedly collected of circadian rhythms in the use of aspect, slope, elevation, and habitat associations by caribou. Specifically, caribou utilized unvegetated areas, high elevations, steep slopes, and northeastern aspects at midday while lower elevations, flatter slopes, varied aspects, and vegetated areas were occupied in the morning and evening (Fig 4.1 - 4.4). With regard to the apparent rhythm of the daily selection process, and the apparent unison choice of specific topographic and vegetation features, it is worth noting that certain variables vary synchronously. That is to say, habitat associations selected by caribou exist only within certain environmental conditions, and thus the interplay between habitat parameters may not always allow a researcher to determine if a caribou prefers one location of its range because of, or despite, the topography and vegetation that occurs there.

With this in mind, the diurnal use of habitat is apparently synchronous with daily temperature patterns, demonstrated by the correlation of both altitudinal movements and slope selection with temperature (r=0.685, p=0.000, and r=0.762, p=0.000 respectively). With regard to habitat associations, caribou were consistently found on late-lying snowpatches, and bare unvegetated slopes between 1100 and 2100, the warmest part of the day (Fig. 4.4, 3.6). Descriptions of similar preferences are common throughout the literature as caribou are known to seek out relief habitat such as snowpatches, windy ridgetops, sandpits, logging roads, river ice, and beaches to escape harassment when insects are active (White *et al.* 1975, Roby 1978, Downes *et al.* 1986, Ion & Kershaw 1989, Russell *et al.* 1993). Given the correlation between insect activity and temperature reported in the literature (Roby 1978, Helle & Tarvainen 1984), and the daily temperature patterns obtained from automated recording stations in this study (Fig. 3.6), it is not difficult to associate the midday movement of caribou into high elevation areas where snowpatches persist on steep, north-facing slopes with a diurnal increase in insect activity. Observations of insect avoidance behaviour further support this belief, as harassment was highest at mid-morning and late-afternoon, times when caribou are presumably moving on

and off snowpatches (Fig. 3.3). Selectivity for bare or snowy habitats was very strong at these times (Fig. 4.4).

During the mornings and evenings, caribou were less selective of a larger variety of habitat associations; however, they had a particular preference for alpine forb meadows (Fig. 4.5 - 4.8). As well, caribou tended to utilize lower elevations, shallower slopes, and a larger variety of aspects during the early and late times of the day. The cool temperatures in the evening and morning were discouraging to insects and made for better conditions to feed, particularly in areas with surface water. At these times, forb meadows, characterized by lush vegetation and moist conditions were highly selected by females. Forb meadows near the Macmillan Pass are characterized by very high productivity (Gill 1978), and several other studies have found forbs to be a preferred plant type of caribou (Stelfox *et al.* 1978, Bloomfield 1980). Skogland (1980) believed that caribou would select habitats characterized by an abundance of forbs in the absence of insect harassment.

Two other vegetation types were selected in the twilight hours (Fig. 4.7, 4.8). Female caribou were seen in areas of lichen-heath which offered little in terms of green forage, but contained an abundance of reindeer lichens (*Cladina* spp.). Alpine lichen-grass communities, similarly depauperate in green vegetation, were also selected prior to 1100 h. Despite the apparent unattractiveness of both these habitat associations for feeding, they may offer some forage for the hungry caribou when insect activity is not conducive to feeding in moist forb meadows. Lichen-heath communities tend to occur on north--facing slopes and alpine lichen-grass is associated with high elevation, windswept terrain (Kershaw & Kershaw 1983), these may act as somewhat transitional habitats for caribou, offering some forage and some relief when insects are still active and caribou are restless to commence or continue feeding. It is also possible that caribou merely passed through these vegetation types as they as they travelled between relief habitat and foraging habitat.

Caribou were rarely seen in shrub communities (Fig. 4.9), despite their apparent affinity for willow browse described in the literature (White *et al.* 1975, Fischer *et al.* 1976, Martell *et al.* 1976, Bloomfield 1980, Skogland 1980). Nonetheless, during several evening surveys, solitary caribou were seen to literally race down from alpine areas, past large aggregations of grazing females and calves, and on out of sight down the mountain. Thus, it is possible that the lack of selection for shrub communities may be due to methodological problems. First, the mountain camps utilized in this study facilitated observation of caribou in alpine areas, and so the reduced lighting at twilight in combination with tall shrubs would make it difficult to see caribou in the birch/willow communities below. In addition, the ratio of alpine habitat to subalpine habitat within any mountain range is skewed such that animals will inevitably be forced to concentrate in areally-restricted high elevation habitats, whereas they will have a greater area to disperse into at low elevation.

Male caribou, in particular, must have been using low elevation shrub habitats at twilight. Over the summer, some 600 caribou observations were collected in alpine habitat prior to 0700 or after 2300 h, however, none of these were bulls, leading to the obvious conclusion that when they were not seeking relief on snowpatches, bulls were somewhere down below (Quayle 1993, unpubl. data). While male caribou share some of the preference exercised by females for alpine forb meadows (Fig. 4.5), they were rarely observed feeding alongside females during the early morning. This leads to speculation that bulls may leave the alpine zone in the late evening, descending to low elevation willow or birch communities. This belief is supported by several anecdotal sightings of bulls along the Tsichu River valley floor by other researchers sharing the base camp with the author; however, no females or calves were ever seen at such low elevations. Other studies near the Macmillan Pass also note that the majority of bulls occur at low elevation (Archibald 1973, Ion 1986). Collin (1983) stated that bulls were conspicuously absent from alpine areas in the study area, and were frequently observed at low elevations, often in riparian areas.

Following this proposition, it appears that both sexes of caribou share a need for relief habitat during the warmest portion of the day. Both are found at high elevation, on steep slopes, and cool, northeastern aspects (Fig. 4.1 - 4.3); females may occupy significantly higher and steeper habitats, but this may be because they do not have to travel as far as males to reach them (Table 4.1, 4.3). Jakimchuk *et al.* (1986) noted that male and female caribou would remain spatially separated in summer, except when aggregating in relief areas in response to insect harassment. Similarly, the most conspicuous difference between habitat selection of male and female caribou occurred in the very late evening, when males apparently left the alpine area altogether. This may be the consequence of another environmental pressure other than insects and temperature.

Vulnerability to predation may constrain the habitat selection of female caribou. It has been asserted that females with calves may avoid certain prime feeding areas, such as low elevation habitats associated with waterways (Bergerud & Page 1987, Jakimchuk *et al.* 1987). It is stated that this avoidance is an attempt for a cow accompanied by a vulnerable calf to minimize the chance of encountering large predators, such as wolves and bears, which travel in valley bottoms. Based on this idea, females with calves are more spatially confined than males, foregoing the freedom to forage in subalpine areas in favour of security from potential predators. This gender-specific resource partitioning may be beneficial by alleviating competition for nutritious, early growth stages of alpine vegetation and thereby increasing the foraging efficiency of lactating mothers and their calves which require fine, concentrated food sources (Jakimchuk *et al.* 1987). In contrast, male caribou are less cautious and may travel down into valleys when insects are inactive, to take advantage of the shrubby vegetation found in riparian areas. Roby (1978) stated that male caribou occupied higher-biomass habitats and spent less time feeding relative to females. He found it curious that cows occupied so-called sub-optimal habitat "...unless there are other overriding factors such as vulnerability to predation of calves." (p. 55).

Predators were present in the study area (Table 4.7). Wolves were sighted on one occasion near the summit dome, but this again may be related more to their visibility at high elevation than to the distribution of wolves. Considering the presence of moose in the valley, 500 vertical meters below, low elevation willow habitats would have seemed a more efficient hunting ground for large game. Although grizzly bears at high elevations might pose a threat to caribou, during one sighting of two grizzlies grazing in a forb meadow, a group of 32 caribou, including 9 calves, rested complacently some 200 m uphill, apparently unconcerned. The bears, likewise, appeared far more interested in grazing forbs than chasing caribou calves. Golden eagles were also sighted in alpine areas favoured by nursery bands of cows and calves.

Perhaps the most voracious predators in the study area were mosquitos. Over the course of the summer, minimum temperatures gradually warmed (Fig. 3.7), creating conditions more favourable to insects. The increase in both temperature and insect abundance lead caribou to the use of significantly higher elevations and significantly steeper slopes (Table 4.2, 4.3). Downes *et al.* (1986) observed a similar progressive movement to higher altitudes by caribou over the fly-season which was negatively correlated with mosquito abundance. Oosenbrug and Theberge (1980) observed a seasonal elevational adjustment which they also attributed to an increase in heat and insect activity. In addition, the use of higher elevations may be a consequence of snowpatch melt at lower elevations, forcing caribou to climb higher to find relief habitat. This is quite probable, given that a significantly higher proportion of caribou were observed on unvegetated areas during the latter half of the study (Table 4.6) despite the intuitively-obvious reduction in the area of snowpatch relief habitat.

## Conclusions

1. Both male and female mountain caribou exhibited a distinct circadian habitat pattern in which they travelled up to higher elevations, steeper slopes, and northeasterly aspects in the afternoon. In the morning and evening, shallower slope angles, lower elevations and varied aspects were utilized.
2. Snowpatches were nearly exclusive preferred habitat for both sexes between 1100 and 1900 h. Forb meadows are preferred in morning by females and in the evening by both males and females. Preference is also shown for alpine lichen-grass areas, and lichen-heath-dominated habitats in morning; however, due to the lack of green vegetation in these communities, it is speculated that they may be transitional habitats which are only utilized when insect activity makes forb meadows less desirable.
3. The circadian habitat cycle of caribou was apparently driven by temperature and concomitant insect activity. Afternoon hours when temperature was greatest were spent in habitats which apparently offered relief from insect harassment. In the evening, when temperatures cooled down and presumably resulted in diminished insect activity, caribou moved down into lush meadows and other areas to feed.
4. Female caribou may have confined themselves to alpine habitats in an effort to protect their calves from predators which travel in valley bottoms. For this reason, they selected alpine forb meadows in both the morning and evening. In contrast, male caribou spent some time grazing in forb meadows in the evening, however, they were never seen in alpine areas between 2300 and 0700 h. It is suspected that during these hours they ventured down into the surrounding valleys to take advantage of lush, riparian habitats.
5. Over the summer, elevation and slope angles that were utilized increased significantly, as did the selection of unvegetated habitats. This is believed to be a response to an increased abundance of insects, and the need to travel higher to find persistent snowpatch relief habitat.

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# Conclusions

## Summary

1. Caribou displayed a distinct circadian rhythm in both activity budgeting and habitat selection (Fig. 5.1). This diurnal pattern appeared to be driven by temperature and its effect on insect activity and harassment.

2. Caribou fed primarily in the morning and evening and demonstrated strong selection of forbs. Forb phytomass appeared to exert some influence over caribou distribution. Females were observed using forb meadows during mornings and evenings, presumably because they were restricted to high elevations as a means of minimizing possible encounters with predators. In contrast, it was suspected that male caribou ventured down to low elevation shrub habitats in the evening, as bulls were never encountered in alpine habitats between 2300 and 0700 h.

3. Caribou were almost exclusively observed standing or lying, often in large groups, on snowpatch habitat at midday. Observations of harassment responses indicated that caribou encountered greatest harassment in the late morning, before moving onto the snow, and in the late afternoon, prior to leaving the snow. Caribou spent a higher percentage of time standing, as opposed to lying down, in the late afternoon, and in the later half of the season. Both were believed to be the result of insect harassment, and possibly the presence of oestrids. Females were observed to spend more time standing than male caribou, possibly as a strategy for coping with flying insect pests in large cow-calf aggregations. Caribou spent a longer amount of time in unvegetated habitats, such as the snowpatch habitat, during the second half of the season, when insects were assumed to be more abundant.

4. Caribou selected habitats at high elevation, based on both pellet-group counts and direct observation. Caribou utilized the highest elevations at midday when temperatures were highest and insects were most active. Throughout the summer, caribou moved to significantly higher elevations presumably in response to increasing temperatures, increasing insect abundance, and decreasing availability of snowpatch relief habitat at lower elevations. Female caribou used significantly higher elevations than did males. Based on phytomass data, caribou appeared to select habitat-types with the least phytomass. This may be a method of avoiding insects and minimizing the chance of ambush by predators, especially for females with calves.

5. Caribou generally selected habitats with steep slopes and northeastern aspects at midday as these areas provided conditions which would discourage flying insects. In the second half of the season, caribou selected significantly higher slopes, likely in response to increasing insect activity due to warmer minimum daily temperatures. Based on pellet counts, caribou utilized areas at high elevation with slope angles <1°, leading to speculation that the use of steep slopes is merely a product of the use of high elevation habitats.

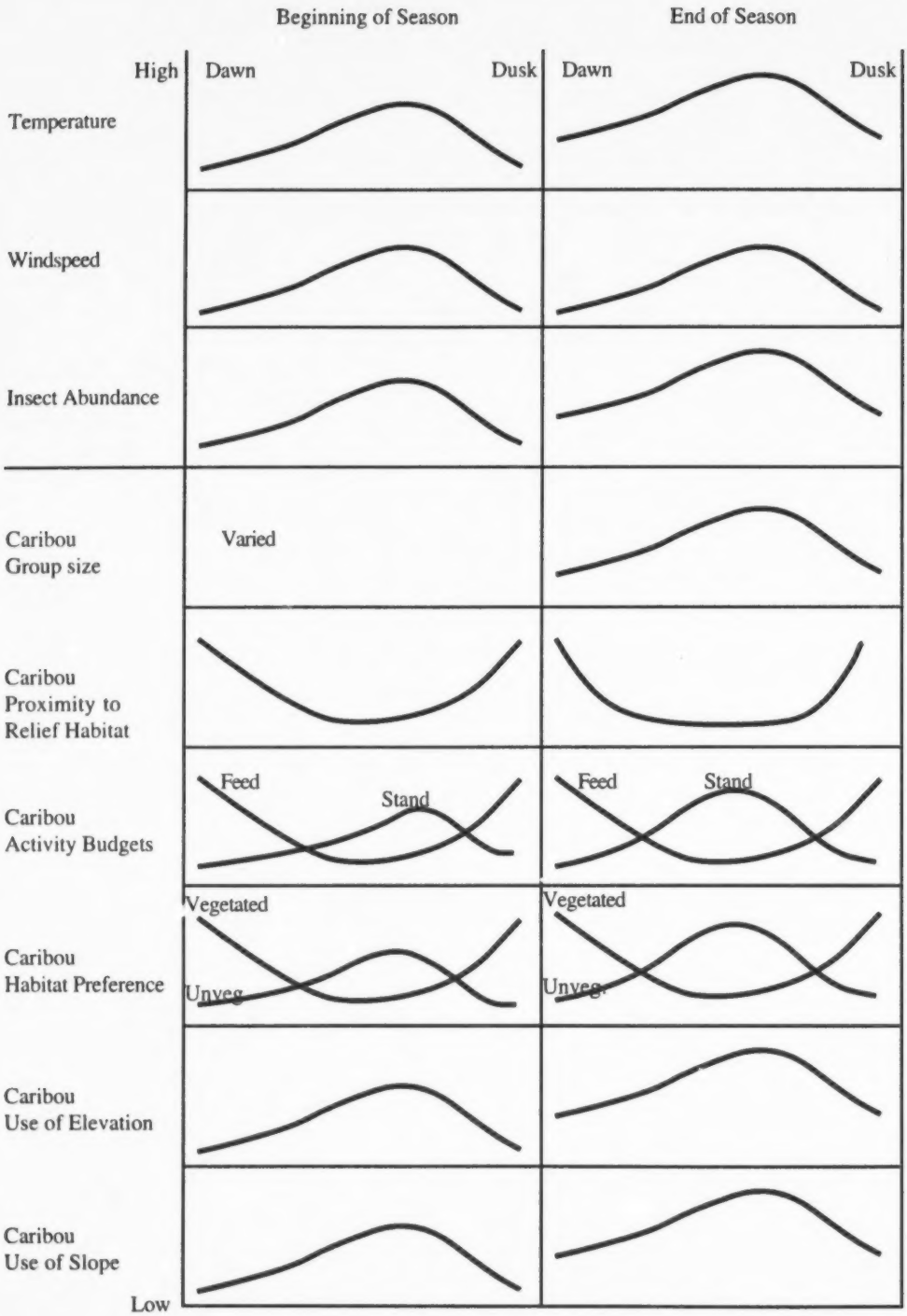


Figure 5.1. Simplified depiction of environmental influences and caribou responses in summer. Each box shows a variable's relative circadian pattern from dusk to dawn. Each column represents one half of the fly-season.

**Synthesis: the diurnal cycle of the mountain caribou**

Summering mountain caribou exhibit distinct and purposeful movements between habitats (Fig. 5.2). Throughout the summer of 1993, a consistent, repeated pattern of habitat use occurred each day, varying slightly depending on conditions.

In the early morning (0500 h), both male and female caribou were repeatedly found grazing in alpine forb meadows, often scattering themselves along water courses and depressional areas. Each morniing as the temperature started to rise (0730 h) and flying insects became active, caribou would cease feeding and begin to travel to higher elevation habitats. At this time of day, long trains of caribou were often seen travelling upslope, stopping occassionally to graze in areas of reduced flying pests until insect harassment would eventually increase sufficiently to drive them higher up the mountainside. Toward late morning, groups of caribou sought relief habitat, and could be seen along ridgetops and on low-lying snowpatches. A large nursery band in the study area was often found on top of a rounded summit dome at this time of day (1100 h), taking advantage of the windswept conditions and apparent reduced insect harassment. Watchful cows, which made up the majority of the group, stood by while their calves lay resting on the tundra or snow. Often one animal appeared like a sentinel, standing alert and watchful at the edge of the summit plateau to prevent threatening intruders from approaching undetected. Bulls, alone or in small groups, were often seen lying on neighboring snowpatches.

Towards late afternoon (1500 h), when the sun became hot and the wind sporadic, caribou would often become restless - stamping, shaking their heads, biting at insect attackers. On particularly warm, calm days, entire groups of caribou might begin to move around, running from one end of the snowpatch to the other as if pursued by oestrid flies, or dispersing to other snowpatches. If insect harassment was too unpleasant, caribou would seek superior relief terrain, often venturing as a group out across an unvegetated saddle of loose rock to the back valley where they travelled high up onto steep, snowy slopes. It is in this extreme habitat that the largest groups of caribou were witnessed, numbering ninety to 175 individuals. They would remain on the snow until early evening (1800 h), showing signs of harassment at intervals, until temperatures would begin to cool when they would disperse downward. Dispersal was often gradual, with animals moving downslope in small, apparently independent groups, taking bites of passing vegetation along the way. On one occasion, a small cloud moving across the sun triggered a group of 26 animals to vacate a snow patch almost immediately.

In the evening (2000 h), female caribou could be seen dispersed and grazing in the forb meadows again. Male caribou were never visible at high elevations late in the evening as they had presumably dispersed into the subalpine shrub communities. Caribou would occasionally appear galloping with considerable urgency down the mountain and into the shrubbery below, apparently moving down to feed in the cool, insect-free evening.

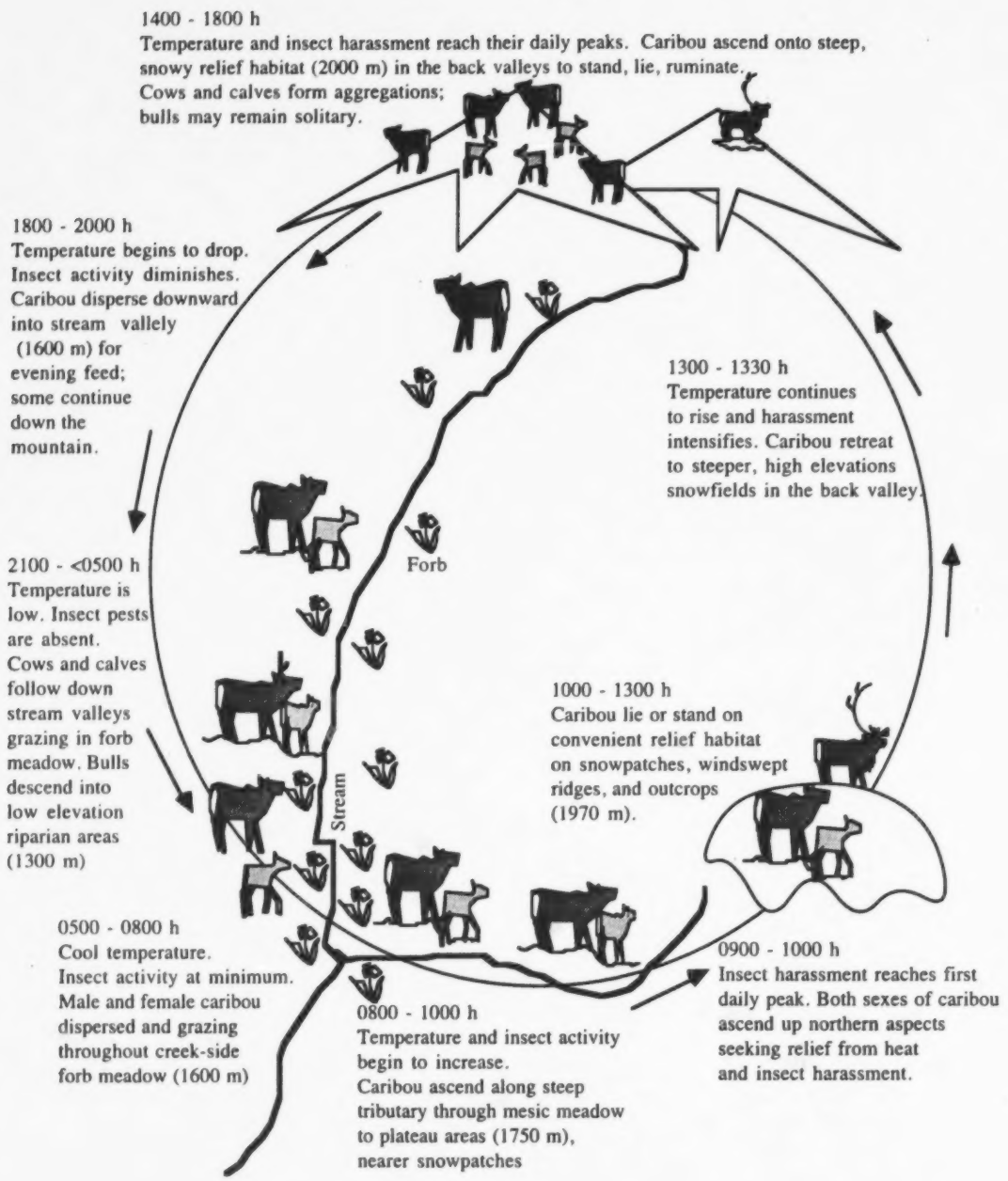
1400 - 1800 h
Temperature and insect harassment reach their daily peaks. Caribou ascend onto steep, snowy relief habitat (2000 m) in the back valleys to stand, lie, ruminate. Cows and calves form aggregations; bulls may remain solitary.
1800 - 2000 h
Temperature begins to drop. Insect activity diminishes. Caribou disperse downward into stream vallely (1600 m) for evening feed; some continue down the mountain.
1300 - 1330 h
Temperature continues to rise and harassment intensifies. Caribou retreat to steeper, high elevations snowfields in the back valley.
Forb
2100 - <0500 h
Temperature is low. Insect pests are absent. Cows and calves follow down stream valleys grazing in forb meadow. Bulls descend into low elevation riparian areas (1300 m)
Stream
1000 - 1300 h
Caribou lie or stand on convenient relief habitat on snowpatches, windswept ridges, and outcrops (1970 m).
0500 - 0800 h
Cool temperature. Insect activity at minimum. Male and female caribou dispersed and grazing throughout creek-side forb meadow (1600 m)
0800 - 1000 h
Temperature and insect activity begin to increase. Caribou ascend along steep tributary through mesic meadow to plateau areas (1750 m), nearer snowpatches
0900 - 1000 h
Insect harassment reaches first daily peak. Both sexes of caribou ascend up northern aspects seeking relief from heat and insect harassment.

Figure 5.2. The diurnal cycle of the summering mountain caribou, based on recurrent observations collected 26 June to 1 August 1993.

## Implications

Habitat selection operates at a number of scales. These range from an animal's macro-perception, such as selecting mountainous terrain for summer range, to the grain of its micro-perception, such as browsing a specific leaf from a *Salix planifolia* plant. Although researchers are fairly confident that they know why it is useful for caribou to differentiate between habitat patches, they are not entirely certain at what scale the most relevant habitat choices occur. Conceptually speaking, each choice at the micro-habitat level is made within the bounds imposed by choices made at the macro-habitat level. This has implications for any habitat study. For example, before this study began, the focal caribou had already selected the study area as summer range, and, thus, the ensuing research was required to operate within the confines of this initial habitat choice. Although caribou are apparently exhibiting habitat selectivity at the scale of this study, they are confined to choosing habitat that lies within the study area.

Perhaps the greatest implications of this thesis do not in fact deal with space, but rather with time. Ecological researchers have long been concerned with change over time, but more in a broad sense, from field season to field season, rather than in terms of diurnal patterns. In a recent article, Schooley (1994) points out some of the weaknesses in amalgamating habitat use data from different years. He states that pooled data may conceal habitat selection patterns occurring at smaller scales, and that a more mechanistic approach, whereby data are collected on both influential and responsive variables, may be the most efficient way to gain useful knowledge. One might examine Schooley's ideas in the context of this thesis, and ponder the potential inaccuracies of amalgamating data over different times of day. As discussed in the final paper of this thesis, habitat studies are rare in which the time of day is considered in the collection, and particularly the analysis, of the data. Amalgamation of hourly data may be automatic, creating a tremendous potential to mask, or even ignore, habitat patterns which operate at the diurnal temporal scale. This may be particularly true at present, when a proliferation of wildlife technology has made it possible to collect large amounts of habitat use data with a minimum of visual contact with the study animal.

The conclusions of this study make it apparent that habitat is not only a spatial concept but a temporal one as well. It is not sufficient to define an animal's habitat preferences merely in terms of location or vegetation type, as the interaction between an animal and its environment is a dynamic, continuous process. Obviously, it is simply not possible, nor useful, to learn a creature's habitat needs for every second of its life; however, I believe the circadian rhythms of an animal's behaviour and habitat use are essential in defining its ecological identity. As an example, the habitat preference of caribou changes from a near exclusive selection of steep, windswept, snowpatches to a strong selection of moist, flat forb meadows within a period of several hours. Neither snowpatches nor forb meadows alone accurately reflect the ecology of the mountain caribou, but when taken together and placed in the context of even a single day, they provide a much greater understanding of how the species interacts with its environment.

Finally, I shall make a personal comment. The mechanistic nature of this study lends itself well to the drawing of conclusions about how one factor influences another, and is definitely worthy of further study. However, despite the collection of over 10,000 observations and the evaluation of multiple statistical hypotheses, I have still witnessed caribou lying up on the snow in the middle of the day in a freezing drizzle when not a mosquito could be seen, or grazing complacently on a field of forbs while clouds of insects buzzed in the air. From an intuitive standpoint, I believe that microhabitat selection by caribou in the Mackenzie Mountains might well prove to be driven more by a circadian rhythm, or habit, than by insects, predators, or any meteorological phenomena. In the Macmillan Pass area, caribou may move up onto the snowpatches in the afternoon simply because that is the way it has always been.

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